The evolution of head structures in Acercaria (Insecta)

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1. Introduction

1.1 The traditional taxa of Acercaria

Acercaria (= Paraneoptera excluding Zoraptera) is a megadiverse group of about 113.000 insects species (e.g. Königsmann 1960; Willmann 2005). Its monophyletic origin was widely accepted (e.g. Kristensen 1981, 1991; Beutel et al. 2013a) and is suggested by the reduced number of tarsomeres, the absence of cerci, the complete ganglionic fusion in the abdomen, the partial reduction or absence of labial palpi, the asymmetric mandibles (ground plan), the slender, chisel- or stylet-like laciniae, the enlarged postclypeus, the reduced number of Malphigian tubules (four or less), the absence of sternum I, spermatozoa with two flagella, and the fusion of the gonangulum with tergum IX (for a summary see Kristensen [1981], Grimaldi & Engel [2005] or Beutel et al. [2013a]). Acercaria comprise the three monophyletic subgroups Psocodea (including Psocoptera with ca. 4.400 species and Phthiraptera with ca. 5.000 species), Thysanoptera (ca. 6.000 species), and Hemiptera (including Auchenorrhyncha with ca. 42.550 species, Sternorrhyncha with ca. 16.400, Heteroptera with ca. 40.500, and Coleorrhyncha with only 36) (e.g. Deckert & Göllner-Scheiding 2005; Grimaldi & Engel 2005; Günther 2005; Larivière et al. 2011; Mey 2005; Mound 2007; Strümpel 2005a, b, c; zur Strassen & Göllner-Scheiding 2005).

Introducing the subgroups of Acercaria is a challenging task. It is a lineage with a remarkably high diversity in its morphology and biology. This includes the feeding habits and host selection, and consequently the structure of the mouthparts. The broad range covers moderately specialized biting and chewing in the detritophagous Psocoptera, punching and sucking in the more or less omnivorous Thysanoptera, highly specialized piercing and sucking in the exclusively phytophagous Sternorrhyncha and Auchenorrhyncha, and ectoparasitism and blood-sucking in Anoplura and a subordinate group of Heteroptera (Grimaldi & Engel 2005). The habitus can be more or less generalized as in the case of the moderately specialized Psocoptera, or strongly modified as in the dorso-ventrally flattened and flightless parasitic lice Phthiraptera or the greatly miniaturized Thysanoptera. Hemiptera evolved a tremendous variety of body shapes including bizarre modifications (e.g. Membracidae, Auchenorrhyncha; Prud'homme et al. 2011) and conspicuous color patterns (Cicadellinae, Auchenorrhyncha; Pyrrhocoridae, Heteroptera). Furthermore, aside from free-living terrestrial species, aquatic or semi-aquatic forms occur (Heteroptera), highly specialized plant feeders (e.g. hemipteran and thysanopteran groups), and ectoparasitism of vertebrates (Phthiraptera; probably with several independent shifts to endoparasitism; summarized in Smith [2003a] and Mey [2005]).

Psocopterans represent the most plesiomorphic morphological condition within Acercaria, resembling superficially a generalized insect. They comprise the traditional subgroups Psocomorpha (bark lice), Troctomorpha (book lice), and Trogiomorpha (bark lice) (summarized in Smithers [1972]; see also Günther [2005]; Beutel et al. [2013a]). Psocoptera are cryptic insects with a worldwide distribution, most speciose in tropical regions, and with some species regularly associated with human habitations (Günther 2005). Some species of Psoquillidae, Lepidopsocidae (Trogiomorpha) (Smithers 1972), Pachytroctidae (Troctomorpha) (Smithers 1972), and Lachesillidae (Psocomorpha) (Günther 2005) occur in nests of ants, birds, or rats, arguably preadaptations to ectoparasitism. The body ranges in size from 0.5 mm to 5 mm, with a brownish coloration or camouflage patterns in most cases (Smithers 1972; Günther 2005). Potential apomorphies of Pscoptera are forewings with an "areola postica" cell, the Pearman's organ on the hind coxa for stridulation (summarized in Grimaldi & Engel 2005), and eggs with a delicate chorion and missing micropyles and aeropyles (Seeger 1979). However, these characters are questionable as current cladistic analyses confirm the paraphyly of this taxon (see 1.2). The fossil record goes back to the Lower Permian (summarized in Smithers 1972; Günther 2005). The oldest and most "primitive" Liposcelididae (Troctomorpha) was found in the Middle Cretaceous Burmese amber (Grimaldi & Engel 2006).

Phthiraptera are highly specialized obligatory ectoparasites of birds and mammals (Mey 2005). The distribution is also worldwide. Traditionally the group is subdivided into the "Mallophaga" or "chewing lice" (Amblycera, Ischnocera), the "sucking lice" (Anoplura) and the "elephant- and wart-hog lice" (Rhynchophthirina) (e.g. Durden 2002; Mey 2005). The body is strongly adapted to the parasitic lifestyle and flattened dorso-ventrally, well sclerotized, equipped with specialized clamp-like tarsi, and wingless (Mey 2005; Friedemann et al. 2013). Further apomorphic characters listed by Grimaldi & Engel (2005) are the partial or complete reduction of the eyes, maxillae, dorsal tentorial arms, ocelli, antennae, and metathoracic spiracles. The eggs are equipped with a hydropile and an operculum and are cemented to the host hair or feather (nits) (Mey 2005). The third thoracic ganglion is fused with the abdominal ganglionic complex (Grimaldi & Engel 2005). The phylogeny of Phthiraptera is currently discussed controversially. It was suggested that the group may not be monophyletic (Johnson et al. 2004; Yoshizawa & Johnson 2006). The body size ranges from 0.35 mm to 11.8 mm (Mey 2005). The fossil record of Phthiraptera is very fragmentary. The oldest amblycerans likely date back to the Eocene (Wappler et al. 2004; Dalgleish et al. 2006). A nit on a mammal hair was found in Baltic amber, also from the Eocene (Mey 2005).

Psocoptera + Phthiraptera form a clade Psocodea with the following apomorphies summarized in Grimaldi & Engel (2005): simplified ovipositor, tear-off device at the antenna, prominent postclypeus, cranial water-vapor absorption system, and absence of the cardo.

Thysanoptera have a worldwide distribution. The small insects are passively transported as aerial plankton and on imported and exported plant products. *Frankliniella occidentalis* (PERGANDE, 1895), for instance, was originally a faunal element of North America but was introduced to Europe in the 1980s in the baggage of horticulture (Moritz 2006). Thysanoptera is composed of two subgroups (Crespi et al. 1996; Buckman et al. 2013). Terebrantia comprises eight extant families with a total of ca. 2.400 species, whereas the single family Phlaeothripidae with ca. 3.500 species is assigned to Tubulifera (Moritz 2006; Buckman et al. 2013). The classification of the families is highly controversial and dynamic. Mound & Morris (2007), for instance, suggested "Terebrantia […] paraphyletic with Tubulifera nested within" based on 18S rDNA. Apomorphies of Thysanoptera are the asymmetric mouthparts (e.g. Mound & Heming 2000), the structure of the base of the forewing (Yoshizawa & Saigusa 2001), and an eversible pretarsal arolium (e.g. Friedemann et al. 2013). The eponymous fringed wings (Moritz 2006) also occur in small species of other groups such as Lepidoptera (Alucitidae, Fazekas 2010), Hymenoptera, and Coleoptera (summarized in Sudhaus & Rehfeld 1992). The body is usually slender and dorso-ventrally flattened, ranging in size from 0.5 to 15 mm (Mound & Heming 2000; Moritz 2006). The oldest unambiguous fossils are from the late Carnian Triassic (Grimaldi et al. 2004; see also Moritz 2006 for a summary of ambiguous fossil thrips).

Hemiptera (Rhynchota) are the largest group within Acercaria and have a worldwide distribution. They occur in a broad spectrum of environments including limnic and marine habitats (Strümpel 2005a). Evans (1963) described them as "the most isolated phylogenetically of all orders of insects", and Kristensen (1981) as the most successful non-holometabolan lineage. The monophyly of Hemiptera is well supported by cladistic analyses of molecular data (e.g. 18S rRNA, Kjer 2004; 18S rDNA, Yoshizawa & Johnson 2005) and morphology. Apomorphies are the absence of maxillary and labial palps and a tube-like labial rostrum composed of several segments (usually four) and containing the mandibular and maxillary feeding stylets (e.g. Grimaldi & Engel 2005; Beutel et al. 2013a). The four traditional subgroups are Sternorrhyncha (Aphidoidea [aphids], Aleyrodoidea [whiteflies], Psylloidea [plant lice], and Coccoidea [scale insects]), Auchenorrhyncha (Cicadomorpha: Cicadoidea [cicadas], Cercopoidea [froghoppers, spittlebugs], Membracoidea [leafhoppers, treehoppers]; Fulgoromorpha [planthoppers]), Heteroptera (true bugs: Enicocephalomorpha, Dipsocoromorpha, Leptopodomorpha, Gerromorpha, Nepomorpha, Pentatomomorpha, Cimicomorpha), and Coleorrhyncha (Peloridiomorpha, moss bugs) (e.g. Grimaldi & Engel 2005). The hemipterans excluding Heteroptera and Coleorrhyncha were traditionally grouped as "Homoptera" (e.g. Muir & Kershaw 1912; Muir 1923; Butt 1943; Evans 1963), a lineage which is likely paraphyletic (e.g. Gullan 1999; Grimaldi & Engel 2005). Paraphyletic taxa are labeled with quotation marks in the following. The oldest hemipteran fossils are

Coleorrhyncha known from the Upper Jurassic to Lower Cretaceous (summarized in Spangenberg et al. 2013a).

Many phytophagous hemipteran species are of great economic importance as agricultural and horticultural pests (e.g. O'Brien & Wilson 1985; Nielson 1985; Backus et al. 2006a). They affect the plant directly by mechanically damaging its surface and vessels, by injection of phytotoxic saliva, and by sucking essential plant nutrients (summarized in Hunter et al. 1996). Additionally, many species (e.g. in Aleyrodidae [Sternorrhyncha]) excrete honey dew which can lead to fungal infections (see Hunter et al. 1996). The most serious problem is the transmission of diseases and viruses as contaminants of the mouthparts (Miles 1968, 1972), even though the infectivity is lost during moulting (Miles 1972). The transmission of pathogens is apparently restricted to Sternorrhyncha (aphids, whiteflies) and Auchenorrhyncha (e.g. Gullan & Cranston 2005; Rodrigo & Purcell 2006). The absence of the capacity to transmit plant-pathogenic viruses in Heteroptera is likely due to the stylet movement during piercing and sucking. The stylets of heteropterans are located between the cells during feeding, whereas those of Sternorrhyncha are inserted into the cells and those of Auchenorrhyncha usually into xylem- or phloem-vessels (Schaefer & Panizzi 2000). Thysanopteran species can also be important plant pests. The symptoms are caused by direct mechanical damage, gall induction and transmission of infectious agents such as the tomato spotted wilt virus (summarized in Mound & Heming 2000; see also Ullman et al. 1989). In terms of the total number of thrips species the number of vectors is relatively small (less than 0.2%), restricted to Thripinae (Thripidae, Terebrantia), and the capacity has likely evolved several times independently (Mound 1995, 2002). Within Hemiptera only heteropteran species (e.g. Cimicidae, Reduvidiidae) affect humans and other vertebrates causing mainly irritations of the skin (Butt 1943). Reduviidae of the genera *Triatoma*, *Rhodnius, Dipetalogaster*, and *Panstrongylus* are vectors of *Trypanosoma cruzi* CHAGAS, 1909 (Kinetoplastida) causing the Chagas' disease. The infection is accomplished with excrements dropped near the puncture immediately after blood sucking (Mehlhorn & Piekarski 2002).

Among Psocodea the most serious pests of humans and other vertebrates are found in Phthiraptera. Psocopterans can be of economic importance in the case of mass reproduction and association with stored products or insect collections (Smithers 1972). Amblycera, Ischnocera, and Anoplura occurring on farm animals in excessive numbers cause irritations of the skin with loss of hairs or feathers, secondary infections and reduced output and profit (Mey 2005). Humans are attacked by five different blood-feeding anopluran species (Mehlhorn & Piekarski 2002) and in exceptional cases by the ischnoceran dog biting louse *Trichodectes canis* (DE GEER, 1778) (Trichodectidae) (Durden 2002). Species of the anopluran genera *Pediculus* and *Phthirus* harm primarily by irritation of the skin and lym-

phoma. Secondary damage is caused by transmitting pathogens that cause the potentially lethal louseborne typhus fever, the potentially lethal relapsing fever, and the benign trench fever by inhalation or scratching of infected feces (Mehlhorn & Piekarski 2002; Mey 2005).

A large amount of information is available on important parasites of plants and humans. Nevertheless the knowledge of the morphological and ecological background is still fragmentary. One important gap is the lack of a comprehensive documentation of the head morphology of the key taxon Liposcelididae (Psocodea), and studies covering cranial soft parts such as musculature, nervous and gland system in basal heteropteran groups, Coleorrhyncha, Auchenorrhyncha, Psocoptera, Ischnocera, and Amblycera. Comprehensive studies documenting the evolution of the mouthparts (also including their musculature) during the transition between different feeding habits are incomplete. In the principal works of Parsons (1964), Matsuda (1965), Puchkova (1970), and Evans (1973) comprehensive morphological data for the key taxa Enicocephalomorpha, Dipsocoromorpha (both Heteroptera), Coleorrhyncha, and Troctomorpha (Psocodea) are missing. This impedes the investigations of functional aspects in Hemiptera as for instance finding the suitable plant tissues (e.g. phloem, xylem) or modes of the formation of salivary sheaths. Another interesting issue is if closely related phytophagous groups feeding on species of different plant lineages, or if alternatively distantly related insects feeding on the same or closely related plants. The anatomical data provided here and the phylogenetic results will help in future studies to address these questions.

1.2 The Phylogeny of Acercaria

There are several ongoing controversies in the phylogeny of Acercaria. Even the monophyly of the group was questioned recently (Yoshizawa & Johnson 2005; Ishiwata et al. 2011; Letsch et al. 2012; Misof et al. subm., 1KITE), although it is supported in several molecular studies (e.g. Wheeler et al. 2001; Xie et al. 2009) and by morphological apomorphies (summarized in Grimaldi & Engel 2005). Considering a paraphylum “Acercaria”, Condylognatha is either sister group to (Psocodea + Holometabola) (Ishiwata et al. 2011; Misof et al. subm.) (Fig. 1C) or a clade ((Condylognatha + Holometabola) + Psocodea) (Fig. 1D) is formed (Yoshizawa & Johnson 2005).

The basal branching pattern, i.a. the relationships between Psocodea, Thysanoptera, and Hemiptera are still questionable. On this issue Kristensen (1991) formulated as follows: “The cautious solution of representing paraneopteran [= acercarian, the author] interordinal relationships as an unresolved trichotomy may be preferable at present.” Other important

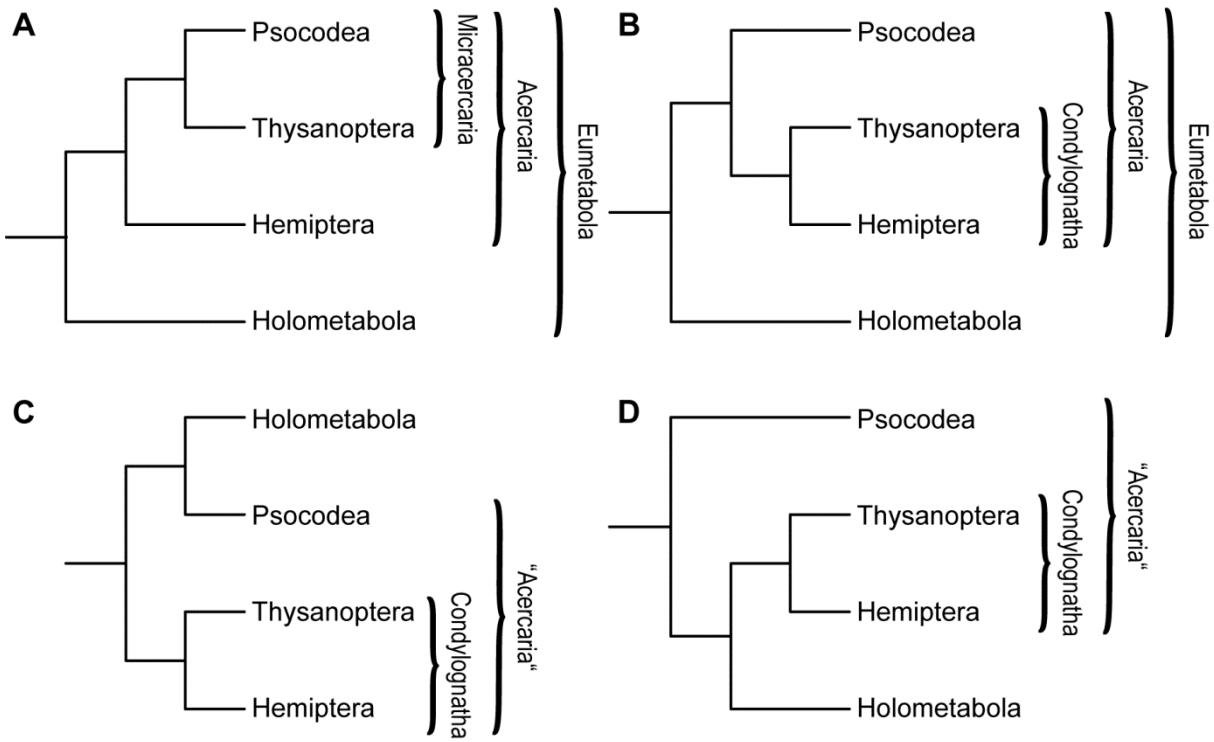

Figure 1. Alternative hypotheses about the phylogenetic position of Thysanoptera. A: The concept of Micracercaria is supported by Bacetti 1979 (spermatological characters), Jamieson 1987 (spermatological characters), Wheeler et al. 2001 (combined analysis of 275 morphological characters, 1000 bases of 18S rDNA, and 350 bases of 28S rDNA), Willmann 2005 (discussion of dorsal cibarial-dilator muscle), Mound & Morris 2007 (cladistic analysis of 1800 base pairs of 18S rDNA), Buckman et al. 2013 (cladistic analysis of 5299 bp from five genetic loci: 18S rDNA, 28S rDNA, Histone 3, Tubulin-alpha I, and cytochrome oxidase c subunit I); B: Evidence for Condylognatha/Hemipteria is presented in Goss 1953 (embryological development), Königsmann 1960 (morphological discussion), Evans 1973 (ontogeny of mouthparts), Seeger 1975 (antennal morphology), Boudreaux 1979, Hamilton 1981 (mouthpart structures), Kristensen 1981, 1991 (mouthpart structures), Lyal 1985 (morphological discussion), Whiting et al. 1997 (combined analysis of 176 morphological characters, 18S rDNA, and 28S rDNA), Yoshizawa & Saigusa 2001 (forewing base structures), Yoshizawa & Saigusa 2003 (structure of maxilla), Johnson et al. 2004 (cladistic analysis of 18S rDNA), Grimaldi & Engel 2005 (mouthpart structures), Moritz 2006 (summary of mouthpart structures), Trautwein et al. 2012 (review of rDNA, nuclear protein-coding DNA), Cui et al. 2013 (cladistic analysis of 13 mitochondrial protein-coding genes), Friedemann et al. 2013 (cladistic analysis of 118 morphological characters including comprehensive data set of tarsal attachment structures); C: Acercaria is shown paraphyletic in the studies of Ishiwata et al. 2011 (cladistic analysis of 3500 amino acid sites) and Misof et al. subm. (1KITE); D: Paraphyletic Acercaria as result in Yoshizawa & Johnson 2005 (cladistic analysis of 18S rDNA).

issues are the monophyly of Phthiraptera, the phylogenetic pattern within the megadiverse Hemiptera, or the monophyly of Auchenorrhyncha.

A major problem is the position of Thysanoptera. In one concept Thysanoptera + Psocodea forming a clade Micracercaria (Fig. 1A) is favored. Potential apomorphies of Micracercaria are the bi-flagellate sperm (Bacetti 1979; Jamieson 1987) and the prominent dorsal cibarial dilator (Willmann 2005). The major support for Thysanoptera + Psocodea comes from analyses of molecular data. This includes studies of Wheeler et al. (2001) (com-

bined analysis of 275 morphological characters, 1000 bases of 18S rDNA, and 350 bases of 28S rDNA), Mound & Morris (2007) (1800 base pairs of 18S rDNA), and Buckman et al. (2013) (5299 bp from five genetic loci: 18S rDNA, 28S rDNA, Histone 3, Tubulin-alpha I, and cytochrome oxidase c subunit I).

In the alternative concept a clade Condylognatha comprises Thysanoptera and Hemiptera (Fig.1B). This group is supported by the similar development of the embryo (Goss 1953) and the ontogeny of mouthparts (Evans 1973). The antennae in both groups are equipped with sclerotized intercalary segments which were interpreted as potential synapomorphies by Seeger (1975). However, Willmann (2005) pointed out the different position in Thysanoptera (between pedicellus and first flagellomere) and Heteroptera (between single flagellomeres) and the doubtful homology. The most conspicuous synapomorphies of Hemiptera + Thysanoptera are the stylet-like laciniae and unicondylar mandibular stylets, the hypognathous head, the expanded hypopharyngeal apodemes, the slender labrum, and the dorsal shift of the anterior tentorial pits (Hamilton 1981; Kristensen 1981, 1991; Grimaldi & Engel 2005). In addition to the characters mentioned above Moritz (2006) reported the presence of a maxillary lever (“Maxillenhebel”) and the reduction of the number of Malphigian tubules. The interpretations of the maxillary stylet and the modifications of the stipes, maxillary palp and galea are uncertain (see below). Yoshizawa & Saigusa (2003) hypothesized the fusion of the galea with the stipes as a potential synapomorphy of Thysanoptera and Hemiptera. Yoshizawa & Saigusa (2001) suggested two potential apomorphies of the forewing base, i.e. the fusion of the basisubcostale with the second axillary sclerite and the distal median plate placed next to the second axillary sclerite. The most recent morphological study supporting a sister group relationship Thysanoptera + Hemiptera was conducted by Friedemann et al. (2013) using 118 characters of the head, thorax, abdomen and tarsal attachment structures of the midlegs. The morphological concept of Condylognatha was also accepted by Hennig (1969), Boudreaux (1979) and Lyal (1985). The monophyly of Condylognatha was also supported in some molecular studies including analyses of 18S rDNA + 28S rDNA (Whiting et al. 1997), 18S rDNA (Johnson et al. 2004; Yoshizawa & Johnson 2005), nuclear protein-coding gene sequences (Ishiwata et al. 2011), mitochondrial protein-coding genes (Cui et al. 2013) and a special box D3-4 of 28S rRNA (Wang et al. 2013). Trautwein et al. (2012) reviewed the present molecular (rDNA, nuclear protein-coding DNA) and morphological evidence in support for Hemiptera + Thysanoptera. The cladistic analysis of Murrell & Barker (2005) (SSU 18S rDNA) also yielded Thysanoptera as sister group to Hemiptera. However, the latter group was displayed as paraphyletic which is totally in contrast to the widely accepted monophyly of Hemiptera (see above).

The phylogenetic controversies also extend to the internal phylogeny of Hemiptera, i.e. the position of Coleorrhyncha and Sternorrhyncha, and the possible paraphyly of

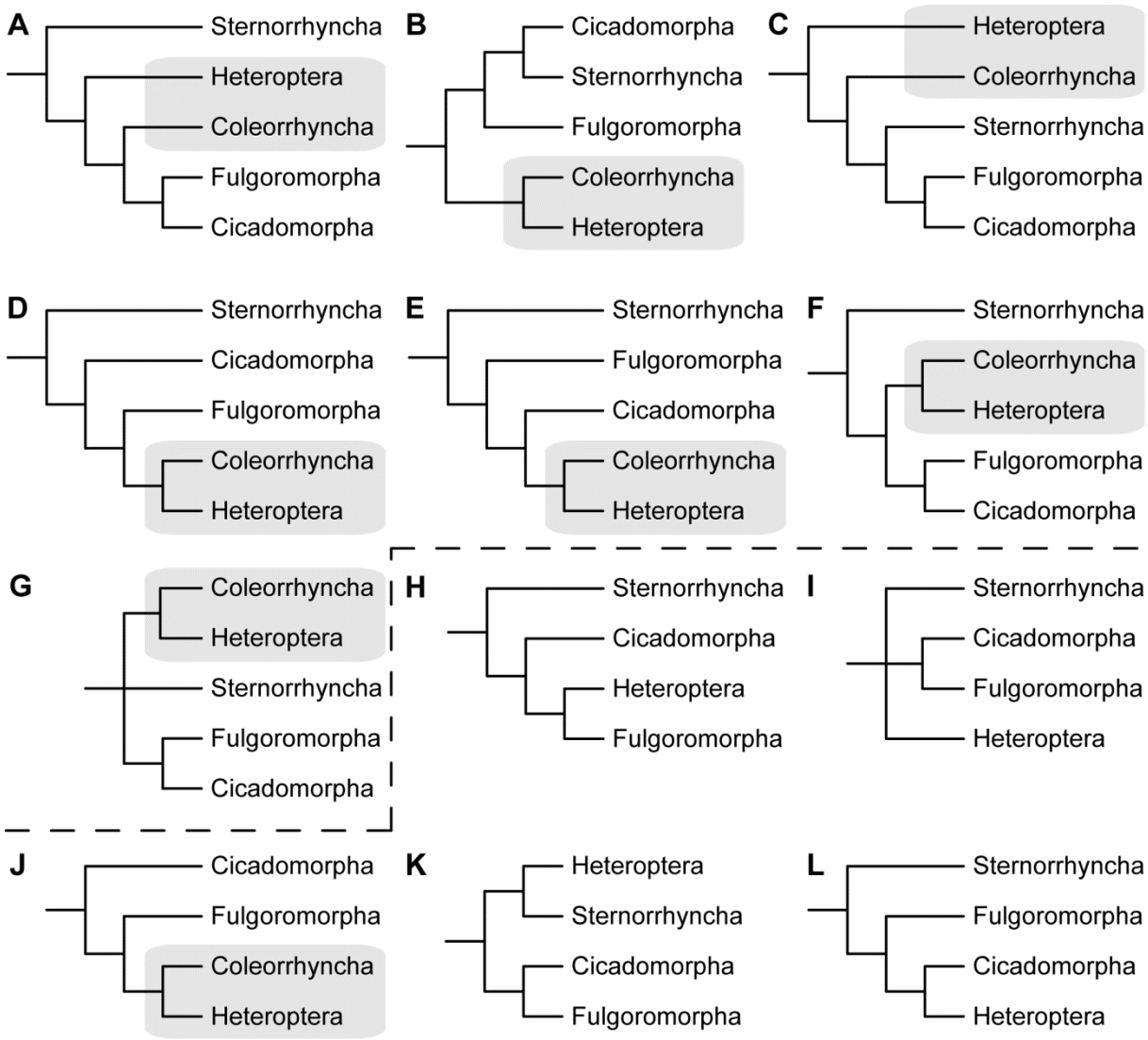

Figure 2. Overview of different phylogenetic relationships among hemipteran taxa, grey box indicates Heteropterodea. The dotted line separates cladograms including a complete taxon sampling above (Sternorrhyncha, Fulgoromorpha, Cicadomorpha, Coleorrhyncha, Heteroptera) from those with an incomplete taxon sampling below. A: monophyletic Auchenorrhyncha and paraphyletic Heteropterodea consistent with Müller 1962 (discussion of hemipteran phyto-endosymbiosis) and Buchner 1965 (discussion of hemipteran phyto-endosymbiosis) in Cryan & Urban 2012; Misof et al. subm. (1KITE), modified; B: paraphyletic Auchenorrhyncha and monophyletic Heteropterodea consistent with Hamilton 1981 (cladistic analysis of head structures), modified; C: monophyletic Auchenorrhyncha and paraphyletic Heteropterodea consistent with Boulard 1988 (morphological discussion) in Cryan & Urban 2012, modified; D: paraphyletic Auchenorrhyncha and monophyletic Heteropterodea consistent with Sorensen et al. 1995 (cladistic analysis of 18S rDNA), modified; E: paraphyletic Auchenorrhyncha and monophyletic Heteropterodea consistent with Bourgoin & Campbell 2002 (review of fossil, molecular, and morphological data) and Xie et al. 2008 (cladistic analysis of SSU nrRNA), modified; F: monophyletic Auchenorrhyncha and monophyletic Heteropterodea consistent with Wheeler et al. 1993 (morphological discussion) and Cryan & Urban 2012 (cladistic analysis of 18S rDNA, 28S rDNA, histone H3, histone 2A, wingless, cytochrome c oxidase I and NADH dehydrogenase, subunit 4) modified; G: monophyletic Auchenorrhyncha and monophyletic Heteropterodea consistent with Friedemann et al. 2013 (cladistic analysis of 118 morphological characters including tarsal attachment structures), modified; H: non-monophyly of Auchenorrhyncha consistent with Campbell et al. 1995 (cladistic analysis of 18S rDNA), modified; I: monophyly of Auchenorrhyncha consistent with Yoshizawa & Saigusa 2001 (cladistic analysis of forewing base structure), modified; J: paraphyletic Auchenorrhyncha and monophyletic Heteropterodea

consistent with Yoshizawa & Johnson 2005 (cladistic analysis of 18S rDNA), modified; K: monophyletic Auchenorrhyncha consistent with Urban & Cryan 2007 (cladistic analysis of 18S rDNA, 28S rDNA, Histone 3, and Wingless), modified; L: paraphyletic Auchenorrhyncha consistent with Letsch et al. 2012 (cladistic analysis of phylogenomic expressed sequence tags data), modified.

Auchenorrhyncha (Fig. 2). The different options for Coleorrhyncha were recently outlined in Spangenberg et al. (2013a) and, thus, only a short summary is presented here. Breddin (1897) suggested a close relationship to the heteropteran Ochteridae. A monophyletic group Coleorrhyncha + Heteroptera (Heteropterodea, Prosorrhyncha) was supported by Schlee (1969), Hamilton (1981), Wheeler et al. (1993), Sorensen et al. (1995), Ouvrard et al. (2000), Bourgoin & Campbell (2002), Schaefer (2009), Cryan & Urban (2012), Friedemann et al. (2013), and Spangenberg et al. (2013a). Alternatively, Coleorrhyncha was considered as part of “Homoptera” with support in Myers & China (1929), Evans (1937, 1957, 1963), Singh (1971), and Boulard (1988).

The monophyly of Auchenorrhyncha is debated since almost 100 years. In one of the first comprehensive morphological studies addressing the hemipteran phylogeny, Muir (1923) proposed a pattern Heteroptera + (Fulgoromorpha + (Cicadellidae/Cicadomorpha + ((Membracidae, Cicadidae, Cercopidae/Cicadomorpha) + Sternorrhyncha))), implying paraphyletic Auchenorrhyncha. Cicadomorpha were also shown as paraphyletic, whereas presently the monophyly of Cicadomorpha (Clypeorrhyncha) and Fulgoromorpha (Archaeorrhyncha) is widely accepted (e.g. Carver et al. 1991; Cryan 2005; Cryan & Urban 2012). The concepts with paraphyletic Auchenorrhyncha strongly differ in the position of Fulgoromorpha and Cicadomorpha. In the morphology-based analysis of Hamilton (1981) a clade of ((Cicadomorpha + Sternorrhyncha) + Fulgoromorpha) + (Coleorrhyncha + Heteroptera) is presented (Fig. 2B). In other studies only Sternorrhyncha forms the most basal branch, with either Cicadomorpha as sister group to the remaining Hemiptera (Sorensen et al. 1995) (Fig. 2D) or alternatively Fulgoromorpha (Bourgoin & Campbell 2002; Xie et al. 2008) (Fig. 2E). Some studies supporting the non-monophyly of Auchenorrhyncha lacked a representative taxon sampling. This includes Bourgoin (1993), Campbell et al. (1994, 1995) (Fig. 2H), von Dohlen & Moran (1995), Hamilton (1996), Bourgoin et al. (1997), Yoshizawa & Johnson (2003, 2005) (Fig. 2J), and Letsch et al. (2012) (Fig. 2L). Other studies support the monophyly of Auchenorrhyncha. Early evidence was presented in an analysis of hemipteran phyto-endosymbiosis (Müller 1962; Buchner 1965) supported by an identical hemipteran cladogram yielded recently from KITE (Misof et al. subm.) (Fig. 2A). A sister group relationship Fulgoromorpha + Cicadomorpha was also confirmed by Boulard (1988) (Fig. 2C). The combined analysis of Wheeler et al. (1993) (31 morphological character, 18S rDNA) and the comprehensive molecular study of Cryan & Urban (2012) (DNA nucleotide sequence data from seven gene regions) (Fig. 2F) yielded further support for the monophyly of Auchenorrhyncha. This was additionally supported by cladistics analyses of a broad

morphological data set including attachment structures (Friedemann et al. 2013) (Fig. 2G). Monophyletic Auchenorrhyncha were also discussed in Kristensen (1975), Carver et al. (1991), Yoshizawa & Saigusa (2001) (Fig. 2I), Grimaldi & Engel (2005), Urban & Cryan (2007) (Fig. 2K), and Buckman et al. (2013).

As in the case of Hemiptera the higher-level phylogeny of Psocodea is still discussed controversially, especially with respect to the monophyly of Psocoptera and Phthiraptera, and whether one of them may be subordinate within the other. In the traditional concept Psocoptera comprises Trogiomorpha + Troctomorpha + Psocomorpha (Smithers 1972; Seeger 1979; Günther 2005), and forms the sister group to monophyletic Phthiraptera (e.g. Lyal 1985; Kristensen 1991; Wheeler et al. 2001; Johnson & Whiting 2002; Smith 2003b) (Fig. 3A). A sister group relationship Ischnocera + Rhynchophthirina suggested by Kim & Ludwig (1978), and a basal position of Anoplura within Phthiraptera (Kim & Ludwig 1982) was not confirmed (see also Fig. 3). Lyal (1985), based on morphological data, pointed out the importance of Liposcelididae (= Liposcelidae, see Smithers 1972) (Troctomorpha) and its possible sister group relationship to Phthiraptera. The latter concept was supported by the same number of apomorphies as monophyletic ("holophyletic") Psocoptera. This suggested a possible alternative psocodean phylogeny with paraphyletic Psocoptera and polyphyletic Phthiraptera. A clade Phthiraptera + Liposcelididae (Troctomorpha) was also supported in Cruickshank et al. 2001 (elongation factor 1α gene) and Yoshizawa & Johnson (2003) (mitochondrial 12S and 16S rDNA). However, the analysis of the latter resulted in polyphyletic Ischnocera and Trogiomorpha, challenging the widely accepted monophyly of these groups (e.g. Johnson & Whiting 2002; Murrell & Barker 2005; Yoshizawa et al. 2006). The studies of Kjer (2004) (18S rRNA) and Johnson et al. (2004) (18S rDNA) strengthened the placement of Liposcelididae as sister group of Phthiraptera. However, the cladogram of the latter shows a pattern (Amblycera + Liposcelididae) + Pachytroctidae (Troctomorpha), the paraphyly of Troctomorpha, the paraphyly of its subgroup Nanopsocetae (Liposcelididae, Pachytroctidae, Sphaeropsocidae), and even the paraphyly of the family Pachytroctidae (Fig. 3B). Trogiomorpha is placed at the base of Psocodea with Psocomorpha as second branch and Amphientometae (Troctomorpha) as sister group to the following Phthiraptera (Fig. 3B). The cladogram of Yoshizawa & Johnson (2005) also shows an arrangement (Amblycera + Liposcelididae) + Pachytroctidae. In contrast to Johnson et al. (2004) Psocomorpha and Amphientometae are placed as sister groups (Fig. 3C). The cladistic analysis of the male genitalia by Yoshizawa & Johnson (2006) also supported a clade (Pachytroctidae + Liposcelididae + Amblycera) (Fig. 3D). The most recent and comprehensive approach to resolve the higher-level phylogeny of Psocodea is Yoshizawa & Johnson (2010). The cladistic analysis of nuclear 18S rDNA, Histone 3, wingless, mitochondrial 16S rDNA and COI gave strong evidence to paraphyletic Psocoptera and a placement of Amblycera outside of

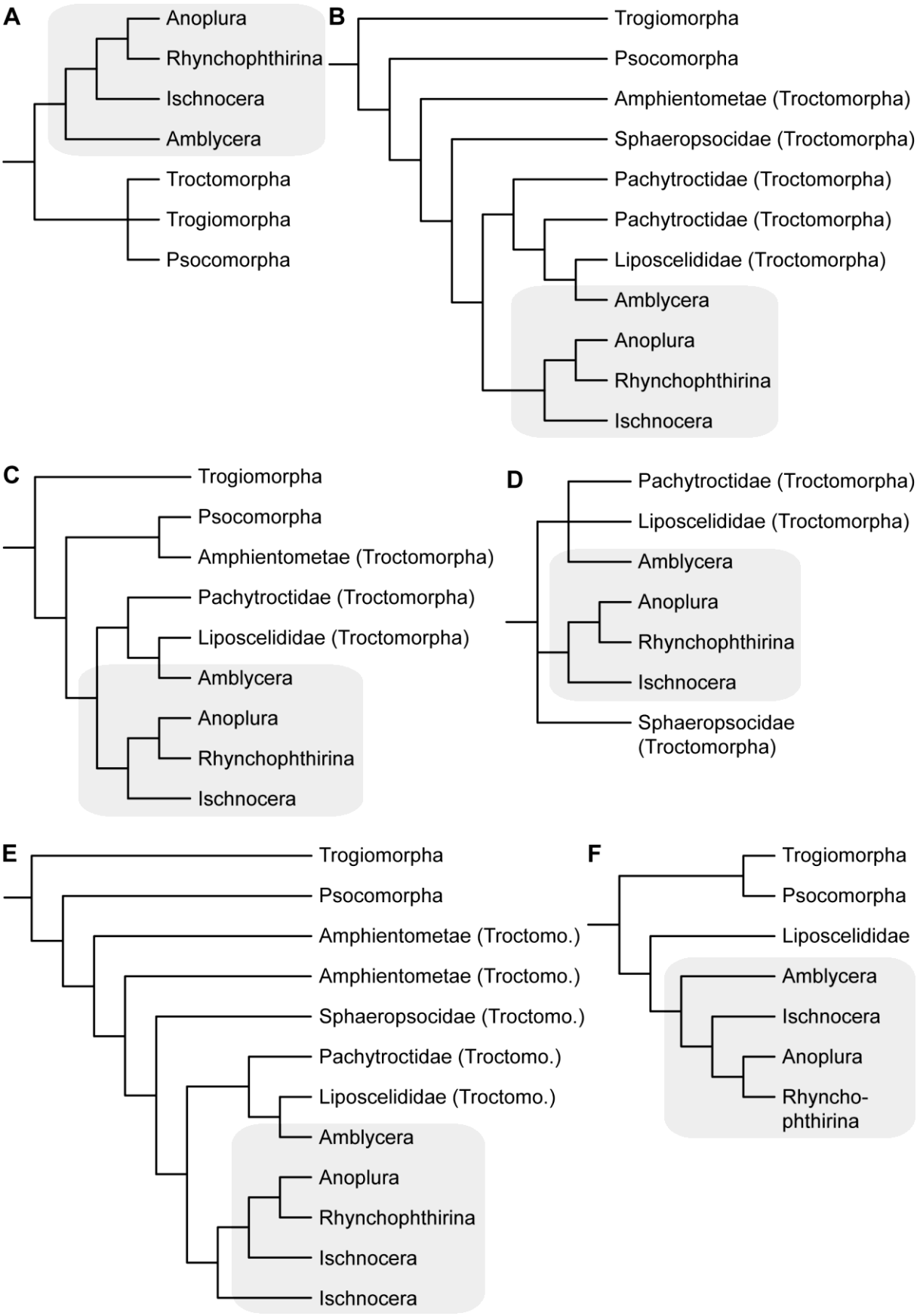
A
Anoplura
Rhynchophthirina
Ischnocera
Amblycera
Troctomorpha
Trogiomorpha
Psocomorpha
B
Trogiomorpha
Psocomorpha
Amphientometae (Troctomorpha)
Sphaeropsocidae (Troctomorpha)
Pachytroctidae (Troctomorpha)
Pachytroctidae (Troctomorpha)
Liposcelididae (Troctomorpha)
Amblycera
Anoplura
Rhynchophthirina
Ischnocera
C
Trogiomorpha
Psocomorpha
Amphientometae (Troctomorpha)
Pachytroctidae (Troctomorpha)
Liposcelididae (Troctomorpha)
Amblycera
Anoplura
Rhynchophthirina
Ischnocera
D
Pachytroctidae (Troctomorpha)
Liposcelididae (Troctomorpha)
Amblycera
Anoplura
Rhynchophthirina
Ischnocera
Sphaeropsocidae (Troctomorpha)
E
Trogiomorpha
Psocomorpha
Amphientometae (Troctomo.)
Amphientometae (Troctomo.)
Sphaeropsocidae (Troctomo.)
Pachytroctidae (Troctomo.)
Liposcelididae (Troctomo.)
Amblycera
Anoplura
Rhynchophthirina
Ischnocera
Ischnocera
F
Trogiomorpha
Psocomorpha
Liposcelididae
Amblycera
Ischnocera
Anoplura
Rhyncho-
phthirina

Figure 3 (previous page). Overview of different phylogenetic relationships among psocodean taxa, grey box indicates Phthiraptera. A: traditional concept of monophyletic Psocoptera (consistent with Smithers 1972, morphological discussion) as sister group to monophyletic Phthiraptera (consistent with Lyal 1985, cladistic analysis of 94 morphological characters; Kristensen 1991, morphological discussion; Wheeler et al. 2001, cladistic analysis of 275 morphological characters, 18S rDNA, 28S rDNA; Johnson & Whiting 2002, cladistic analysis of EF1α, 18S rDNA, COI; Smith 2003 (review of molecular and morphological data), modified; B: paraphyletic Psocoptera and polyphyletic Phthiraptera consistent with Johnson et al. 2004 (cladistic analysis of 18S rDNA), Kjer 2004 (cladistic analysis of 18S rRNA), modified; C: paraphyletic Psocoptera and polyphyletic Phthiraptera consistent with Yoshizawa & Johnson 2005 (cladistic analysis of 18S rDNA), modified; D: paraphyletic Psocoptera and polyphyletic Phthiraptera consistent with Yoshizawa & Johnson 2006 (cladistic analysis of morphological characters of male genitalia), modified; E: paraphyletic Psocoptera, paraphyletic Ischnocera and polyphyletic Phthiraptera consistent with Yoshizawa & Johnson 2010, fig. 4 (cladistic analysis of nuclear 18S rDNA, Histone 3, wingless, mitochondrial 16S rDNA and COI) (see also Xie et al. 2009), modified; F: paraphyletic Psocoptera and monophyletic Phthiraptera consistent with Friedemann et al. 2013 (cladistic analysis of 118 morphological characters including tarsal attachment structures), modified.

Phthiraptera (Fig. 3E). As in Johnson et al. (2004) Trogiomorpha, Psocomorpha, and Amphientometae (Troctomorpha) were placed as basal lineages (see also the molecular study of Xie et al. [2009] with limited taxon sampling). Within their extensive taxon sampling Amphientometae and Ischnocera emerged as paraphyletic, respectively. As outlined above the major support for the paraphyly of Psocoptera and polyphyly of Phthiraptera (with Amblycera placed outside) is based on molecular data (see additionally Murrell & Barker 2005; Kjer et al. 2006). The morphological data relevant in this context was quite fragmentary until recently (except for male genitalia, see Yoshizawa & Johnson 2006), but a sizeable morphological matrix was analyzed by Friedemann et al. (2013), a study including a detailed documentation of tarsal and pretarsal attachment structures. Trogiomorpha and Psocomorpha emerged as sister groups placed at the base of Psocodea (Fig. 3F). Psocoptera is paraphyletic and Liposcelididae the sister group to monophyletic Phthiraptera (see also the molecular study Barker et al. [2003] with limited taxon sampling) (Fig. 3F). Wiens et al. (2003) pointed out that the incongruence between morphological and molecular phylogenies is likely due to morphological homoplasy resulting from parallel evolution triggered by similar adaptive zones of the host (e.g. Kim & Ludwig 1978; Smith 2003a; Smith et al. 2004).

1.3 Main issues addressed in this thesis

1. Cephalic anatomy

A detailed documentation of the head morphology including musculature, nervous system, digestive tract and glands is a main part of the present thesis. In total 18 species are studied using mainly semi-thin sectioning, and scanning-electron-microscopy. Additionally, computer-

based 3D-reconstruction is applied which has become well-established in the last decade (e.g. Friedrich & Beutel 2008; Wipfler et al. 2009; Beutel et al. 2010; Wipfler et al. 2011; Spangenberg et al. 2012; Friedrich et al. 2014). The sampling contains the hemipteran key taxa Coleorrhyncha (Spangenberg et al. 2013a), Enicocephalomorpha and Dipsocoromorpha (Heteroptera) (Spangenberg et al. 2013b).

2. Phylogeny

The second main aim is to reconstruct the phylogeny of the subgroups of Acercaria. The morphological dataset obtained from the 18 examined species is combined with morphological data of 54 original studies (including six outgroup taxa) to present a morphological data matrix of 397 potential phylogenetically relevant cephalic characters for 72 species. The phylogenetic results obtained from cephalic morphological information are compared with results of previously published studies (e.g. Friedemann et al. 2013) including also comprehensive molecular approaches (i.a. 1KITE).

3. Character evolution

Scenarios for the evolution of the acercarian heads based on the result of the phylogenetic analysis are discussed, referring in particular to the type of “Psocoptera”, Anoplura + Rhynchophthirina, Thysanoptera, and Hemiptera. One of the central points is the evolution of the hemipteran mandibular and maxillary plates and levers, respectively, and the associated musculature.

4. Ecological aspects

Mapping the feeding modes of the single taxa on alternative cladograms resulted from the present thesis can elucidate the classification of the primitive feeding mode in Hemiptera and Heteroptera (phytophagy/herbivory versus carnivory/predatory). This concerns also potential adaptations to xylem- and phloem-feeding and whether closely related phytophagous insect groups feed on different plant lineages or if distantly related insect groups feed on the same plant.

5. Functional aspects

The uptake of solid and liquid food is compared between the subgroups of Acercaria, with special emphasis on Hemiptera and the development of salivary sheaths in response to different plant tissues.

2. Material and Techniques

2.1 Material examined

Seventy two species were included in the analysis. Original data were obtained for 18 of them (marked by an asterisk). Data for 54 terminal taxa were exclusively taken from detailed original studies (Tab. 1).

2.2 Morphological methods

Scanning electron microscopy (SEM)

Scanning electron (SEM) micrographs were taken with a Philips XL 30 ESEM (FEI Company, Oregon, USA) and Scandium 5.0 Software (Soft Imaging System GmbH, Münster, Germany). Specimens were dried either at the critical point (EmiTech K850, Quorum Technologies, West Sussex, UK) (*Hackeriella*), or using hexamethyldisilazane (for details see Brown 1993) (*Systelloderes, Cryptostemma, Pseudococcus, Dictyophara, Cerobasis, Liposcelis, Piagetiella, Columbicola, Pediculus, Phthirus*) and sputter-coated with gold (EmiTech K500, Quorum Technologies, West Sussex, UK). A rotatable specimen holder was used to mount the sample (see Pohl 2010).

Cross-Section series and computer-based 3D-reconstruction

Specimens were embedded in Araldite® (Huntsman Advanced Materials, Bergkamen, Germany) for semi-thin cross sectioning (1 µm: *Cryptostemma*, *Systelloderes*, *Hackeriella*, *Pseudococcus*, *Philaenus*, *Dictyophara*, *Aleyrodes*, *Cacopsylla*, *Caecilius*, *Cerobasis*, *Liposcelis*, *Piagetiella*, *Columbicola*, *Pediculus* f. body louse) or longitudinal sectioning (1 µm; *Gerris*) with a glass knife on a microtome HM 360 (Microm, Walldorf, Germany). The sections were stained with toluidin-blue. Images of sections for 3D-reconstruction were taken with a Zeiss Axioplan (Zeiss, Göttingen, Germany), the AnalySIS® documentation system (Soft Imaging System GmbH, Münster, Germany) and a pixelink CCD-camera (PixeLINK, Ottawa, Canada). Figures were processed in Adobe® Photoshop® CS2 Version 9.0 (Adobe Systems Incorporated San Jose, California, USA) and Adobe® Illustrator® CS2 12.0.0 (Adobe Systems Incorporated, San Jose, California, USA). Alignment and 3D-reconstructions were done with Mercury Amira® 4.1.2 (Visage Imaging GmbH, Berlin, Germany) and surfaces were smoothed with Autodesk Maya® 7.0 (Autodesk GmbH, Munich, Germany).

Table 1: Taxon sampling and source of data, asterisks indicate specimens studied in present project, sex only mentioned if known.

taxon			literature source
Hemiptera	Heteroptera	Enicocephalomorpha: Enicocephalidae: *Systelloderes* sp.*, Peru: Cuzco: Wayqecha Research Center, 2821 m, 13°10′22″S, 71°35′32″W, 05.12.2011, leg. et det. C. Weirauch, P11L57 sweep, two specimens	---
		Dipsocoromorpha: Dipsocoridae: *Cryptostemma waltli* FIEBER, 1860*, Germany: Mindelsee (Lake Constance), in pitfall traps on a fallow, 24.10.1989, leg. Kiechle, det. R. Heckmann, two specimens.	---
		Dipsocoromorpha: Dipsocoridae: *Hypsipteryx* sp.	Štys 1970
		Dipsocoromorpha: Schizopteridae	Emsley 1969
		Nepomorpha: Ochteridae: *Ochterus marginatus* (LATREILLE, 1804)	Rieger 1976
		Nepomorpha: Corixidae: *Corixa punctata* (ILLIGER, 1807)	Benwitz 1956
		Nepomorpha: Gelastocoridae: *Gelastocoris oculatus* (FABRICIUS, 1798)	Parsons 1958, 1959, 1960a,b
		Nepomorpha: Belostomatidae: *Lethocerus uhleri* (MONTANDON, 1896)	Parsons 1968
		Nepomorpha: Belostomatidae: *Belostoma* sp.	Verma et al. 1973; Swart & Felgenhauer 2003
		Nepomorpha: Belostomatidae: *Hydrocyrius columbiae columbiae* SPINOLA, 1852	Kopelke 1978
		Nepomorpha: Nepidae: *Nepa cinerea* LINNAEUS, 1758	Hamilton 1931; Rieger 1976
		Gerromorpha: Gerridae: *Gerris* sp.*, Germany, Thuringia, Jena, 11°35′07″E, 50°54′23″N, 07.2012, leg. et det. R. Spangenberg, one specimen.	Matsuda 1960; Cranston & Sprague 1961; Andersen 1982
		Gerromorpha: Hydrometridae: *Hydrometra martini* KIRKALDY, 1900	Sprague 1956; Andersen 1982
		Leptopodomorpha: Saldidae: *Saldula pallipes* (FABRICIUS, 1794)	Parsons 1962, 1963
		Cimicomorpha: Reduviidae: *Triatoma infestans* KLUG, 1834	Barth 1952a,b, 1953a,b; Rieger 1976
		Pentatomomorpha: Pyrrhocoridae: *Dysdercus koenigii* Fabricius, 1775	Kumari 1955
		Pentatomomorpha: Pyrrhocoridae: *Dysdercus fasciatus* SIGNORET, 1861	Khan 1972
	Coleorrhyncha	Peloridiidae: *Hackeriella veitchi* (HACKER, 1932)*, two females, Queensland/Australia, Springbrook National Park, Repeater Station, 2006,leg. Geoff Monteith	---
		Peloridiidae: *Peloridium hammoniorum* BREDDIN, 1897*, one specimen (from NP Kristensen, Zoologisk Museum, Copenhagen)	---
		Peloridiidae: *Pantinia darwinii* CHINA 1962*, Chile: IX Reg. Pr. Malleco, PNNahuelbuta, Administración, 37_500S 73_000W 1100 m, 23.12.1992, D. Burckhardt # 30b, det. D. Burckhardt 2009, one specimen	---
		Peloridiidae: *Hemiodoecus leai* CHINA, 1924	Singh 197; Hamilton 1981
	Sternorrhyncha	Aphidoidea: Aphididae: *Aphis fabae* SCOPOLI, 1763	Weber 1928, 1929b; Saxena & Chada 1971; Forbes 1977
		Aphidoidea: Aphididae: *Macrosiphum rosaiformis*/*M. rosae* (LINNAEUS, 1758)	Singh 1971
		Aphidoidea: Phylloxeridae: *Dactylosphaera vitifolii*/*Viteus vitifoliae* (FITCH, 1855)	Breider 1952; Rilling 1960, 1967

Hemiptera	Sternorrhyncha	Aleyrodoidea: Aleyrodidae: *Trialeurodes vaporariorum* (WESTWOOD, 1856)	Weber 1935
		Aleyrodoidea: Aleyrodidae: *Aleurolobus barodensis* (MASKELL, 1896)	Singh 1971
		Aleyrodoidea: Aleyrodidae: *Aleyrodes* sp.*, Germany, Thuringia, Jena-Löbstedt on *Brassica oleracea* var. *botrytis,* 05.07.2012, leg.et det. R. Spangenberg	---
		Psylloidea: Psyllidae: *Psylla mali* SCHMIDBERGER, 1836	Weber 1929a
		Psylloidea: Psyllidae: *Diaphorina citri* KUWAYAMA, 1908	Singh 1971; Garzo et al. 2012
		Psylloidea: Psyllidae: *Cacopsylla* sp.*, Germany, Thuringia, Jena-City on *Crataegus* sp., 05.2011, leg.et det. R. Spangenberg, two specimens	---
		Coccoidea: Coccidae: *Pseudococcus longispinus* (♀) (TARGIONI TOZZETTI, 1867)*, Germany, Saxony, Mitteldorf, on *Phalaenopsis* sp., 25.09.2011, leg.et det. R. Spangenberg, three specimens	---
		Coccoidea: Margarodidae: *Perissopneumon tectonae* (♀) (MORRISON, 1927)	Singh 1971
	Auchenorrhyncha	Cicadomorpha: Cicadoidea: Cicadidae: *Tibicina septendecim* (LINNAEUS, 1758)	Snodgrass 1927; Kramer 1950
		Cicadomorpha: Cicadoidea: Cicadidae: *Platypleura octoguttata* FABRICIUS, 1788	Singh 1971
		Cicadomorpha: Membracoidea: Cicadellidae: *Idiocerus* sp.	Qadri 1949; Arora & Singh 1962
		Cicadomorpha: Membracoidea: Membracidae: *Oxyrhachis tarandus* (FABRICIUS, 1798)	Singh 1971
		Cicadomorpha: Cercopoidea: Aphrophoridae: *Philaenus spumarius* (LINNAEUS, 1758)*, Germany, Thuringia, Jena, grassland, 07.2012, leg. et det.: K. Friedemann, two specimens	---
		Cicadomorpha: Cercopoidea: Cercopidae: *Lepyronia quadrangularis* (SAY, 1825)	Kramer 1950
		Fulgoromorpha: Fulgoridae: *Scolops pungens* (GERMAR, 1830)	Kramer 1950
		Fulgoromorpha: Flatidae: *Melicharia quadrata* MELICHAR, 1903	Singh 1971
		Fulgoromorpha: Dictyopharidae: *Dictyophara europaea* (LINNAEUS, 1767)*, Germany, Thuringia, Jena, Forst, grassland, 31.07.2012, 50°55'12.09"N, 11°33'28.48", leg. et det.: H. Pohl, two specimens	---
Thysanoptera	Terebrantia	Aeolothripidae: *Aeolothrips fasciatus* (LINNAEUS, 1758)	Mickoleit 1963
		Aeolothripidae: *Aeolothrips intermedius* BAGNALL, 1934	Moritz 1982b,c
		Thripidae: *Thrips physapus* LINNAEUS, 1761	Risler 1957; Mickoleit 1961
	Tubulifera	Phlaeothripidae: *Haplothrips statices* (HALIDAY, 1836)	Mickoleit 1961; Mickoleit 1963
		Phlaeothripidae: *Phlaeothrips coriaceus* (HALIDAY, 1836)	Mickoleit 1961; Mickoleit 1963
Psocodea	Psocoptera	Psocomorpha: Psocotae: Psocidae: *Psocus confraternus* BANKS,1905	Cope 1940, see also remarks of Seeger 1975 and Yoshizawa 2005
		Psocomorpha: Psocotae: Psocidae: *Psococerastis nubila* (ENDERLEIN, 1906)	Masumoto & Nagashima 1993
		Psocomorpha: Caeciliusetae: Stenopsocidae: *Stenopsocus stigmaticus* (IMHOFF & LABRAM, 1842)	Badonnel 1934; Matsuda 1965
Psocodea	Psocoptera	Psocomorpha: Caeciliusetae: Caeciliusidae: *Caecilius* sp.*, one specimen	---
		Trogiomorpha: Atropetae: Trogiidae: *Cerobasis* sp.*, Germany, Thuringia, Jena-Löbstedt, sweeping, 09.08.2011, leg. R. Spangenberg, det. E. Anton, two sp.	---

Psocodea	Psocoptera	Troctomorpha: Nanopsocetae: Liposcelididae: *Troctes divinatorius* MÜLLER, 1776	Noland 1924; Chapman GB. 2003; Hu et al. 2009
		Troctomorpha: Nanopsocetae: Liposcelididae: *Liposcelis decolor* (Pearman, 1925)*, USA, Arizona, Oak Canyon, Flag Staff, 10.08.2004, (material of K. Yoshizawa), two specimens	---
	Phthiraptera	Amblycera: Gyropidae: *Gliricola gracilis* NITZSCH, 1818	Risler & Geisinger 1965
		Amblycera: Menoponidae: *Myrsidea cornicis* (DE GEER, 1778)	Mayer 1954; Buckup 1959
		Amblycera: Menoponidae: *Pseudomenopon pilosum* (SCOPOLI, 1763)	Haub 1967
		Amblycera: Menoponidae: *Piagetiella caputincisum* EICHLER, 1950*, on *Phalacrocorax albiventer* (King, 1828), New Island, Falkland Islands, 31.01.2007, leg. HJ van Noordwyk, two specimens	---
		Amblycera: Trimenonponidae: *Trimenopon jenningsi* KELLOG & PAINE, 1910	Stöwe 1943
		Amblycera: Ricinidae: *Trochiloecetes*	Haub 1983
		Ischnocera: Trichodectidae: *Bovicola caprae* (GURLT, 1843)	Risler 1951; Mayer 1954
		Ischnocera: Philopteridae: *Columbicola columbae* EWING, 1929* on *Columba livia domestica* Gmelin, 1789, Germany, Saxony, Adorf/Erzgebirge, 15.10.2011, leg. et det. R. Spangenberg, three specimens including one male	Mayer 1954
		Ischnocera: Philopteridae: *Ornithobius cygni* (LINNAEUS, 1758)	Haub 1971
		Anoplura: Haematopinidae: *Haematopinus suis* LINNAEUS, 1758	Stojanovich 1945; Ramcke 1965
		Anoplura: Hybophthiridae: *Hybophthirus notophallus* (NEUMANN, 1909)	Tröster 1990a,b, 1997
		Anoplura: Pediculidae: *Pediculus humanus* LINNAEUS,1758 (head louse)*, collected of the head of a ten year old boy in Jena, Thuringia, Germany, 2011, leg. H. Reip, two females	---
		Anoplura: Pediculidae: *Pediculus humanus* LINNAEUS,1758 (body louse)*, Florida, USA, and collection of the FSU Jena, 1997, five females and two males	---
		Anoplura: Phthiridae: *Phthirus pubis* (LINNAEUS, 1758)*, collected from a women of uncertain age in Jena, Thuringia, Germany, 1996, two females	Hirsch 1986
		Rhynchophthirina: Haematomyzidae: *Haematomyzus elefantis* PIAGET, 1869	Weber 1939, 1969
outgroup	Hymenotpera	Xyelidae: *Macroxyela ferruginea* (SAY, 1824)	Beutel & Vilhelmsen 2007
outgroup	Neuroptera	Osmylidae: *Osmylus fulvicephalus* (SCOPOLI, 1763)	Beutel et al. 2010
outgroup	Orthoptera	Schizodactylidae: *Schizodacfylus monstrosus* (DRURY, 1770)	Khattar 1964, 1972
outgroup	Ephemeroptera	Oniscigastridae: *Oniscigaster wakefieldi McLachlan,* 1873	Staniczek 2001
outgroup	Plecoptera	Perlidae: *Perla cephalotes* CURTIS, 1827	Chisholm 1962
outgroup	Zoraptera	Zorotypidae: *Zorotypus hubbardi* CAUDELL 1918,	Beutel & Weide 2005

2.3 Cladistic Analysis

The cladistic analysis is based on 397 cephalic characters of 72 species. These characters include the musculature, nervous system, digestive system and salivary system. The tracheal system, the blood system and the antennal heart were not examined in closer detail. Winclada 1.00.08 (Nixon 2002) was used for compiling the matrix and NONA (Ratchet, search settings: 1000 replicates) (Goloboff 1999) and TNT (Goloboff et al. 2008) (Settings Memory: General Ram 200 Mbytes, Max. trees 99999; Analyze Traditional Search, random seed 999999) for calculating minimum length trees. Only unambiguous character transformations were evaluated. Branch support values (Bremer 1994) were calculated with the "Bremer Support" function implemented in TNT (calculate support with TBR, collapse nodes with support below 0, retain trees suboptimal by 30 steps). Characters were coded as non-additive and of equal weight. For additional character evaluations and character mapping alternative topologies were enforced with Winclada ("move branch mode"). The "collapse node mode" was used for collapsing relationships within the infraorders.

2.4 Terminology

The general morphological terminology for the head follows Seifert (2005). Modified structures are specified in detail. The terms dorsal, ventral, anterior and posterior consistently refer to the longitudinal body axis (e.g. vertex dorsal, labium ventral). Muscles are numbered following the terminology of Friedrich & Beutel (2008) and Wipfler et al. (2011). The definition of ridges, sutures and tentorium also follows Wipfler et al. (2011). A suture is interpreted as ecdysial cleavage line whereas a ridge is a cuticular strengthening. The author is trying to avoid terms as order, infraorder, suborder, and superorder. Like all supraspecific entities they are not definable (e.g. Sudhaus & Rehfeld 1992).

3. Results

3.1 Published Results

3.1.1 Overview of Published Results

Study I: **Spangenberg R**, Wipfler B, Friedemann K, Pohl H, Weirauch C, Hartung V, Beutel RG (2013a). The cephalic morphology of the Gondwanan key taxon *Hackeriella* (Coleorrhyncha, Hemiptera). Arthropod Structure & Development 42, 315–337.

Study II: Friedemann K, **Spangenberg R**, Yoshizawa K, Beutel RG (2013). Evolution of attachment structures in the highly diverse Acercaria (Hexapoda). Cladistics 2013, 1–32.

Study III: **Spangenberg R**, Friedemann K, Weirauch C, Beutel RG (2013b). The head morphology of the potentially basal heteropteran lineages Enicocephalomorpha and Dipsocoromorpha (Insecta: Hemiptera: Heteroptera). Arthropod Systematics & Phylogeny 71(2), 103–136.

3.1.2 Study I

Spangenberg R, Wipfler B, Friedemann K, Pohl H, Weirauch C, Hartung V, Beutel RG (2013a). The cephalic morphology of the Gondwanan key taxon *Hackeriella* (Coleorrhyncha, Hemiptera). Arthropod Structure & Development 42, 315–337.

Abstract: External and internal head structures of Coleorrhyncha, a key-taxon within the Hemiptera, are described in detail and documented using modern techniques. The main focus is on *Hackeriella veitchi*, but two additional representatives of the Gondwanan relict group were also examined, and also head structures of Enicocephalidae, a member of a potentially basal heteropteran lineage. Features were compared to those documented in literature for the Sternorrhyncha, Auchenorrhyncha, and Heteroptera. Coleorrhyncha are characterized by highly modified head structures and correspondingly an entire series of autapomorphies, such as for instance a strongly flattened head capsule with fenestrations. However, they also display features that are likely plesiomorphic compared to members of other hemipteran groups. These include the almost complete tentorium and the lack of the gula. The sister group relationship between Coleorrhyncha and Heteroptera is well supported by cephalic features. Potential synapomorphies are the presence of a distinct mandibular sulcus, the reduced number of antennomeres, the absence of clasping organs in the labial groove, coiled accessory salivary ducts, the presence of a small cervical muscle M1a (M. pronotopostoccipitalis medialis), the presence of a second mandibular promoter M14 (M. zygomaticus mandibulae), the presence of M28 (M. verticopharyngalis), and M30 (M. frontobuccalis posterior).

Significance in the present thesis: Coleorrhyncha is a key-taxon within Hemiptera which contributes either to the monophyly or paraphyly of Auchenorrhycnha or to the argumentation of Heteropterodea. This study fills a gap by providing the first detailed and well documented data set of external and internal cephalic structures of a moss bug used for cladistic analysis to resolve internal hemipteran phylogeny.

Own contribution: 80%

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The cephalic morphology of the Gondwanan key taxon *Hackeriella* (Coleorrhyncha, Hemiptera)

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ABSTRACT

External and internal head structures of Coleorrhyncha, a key-taxon within the Hemiptera, are described in detail and documented using modern techniques. The main focus is on *Hackeriella veitchi*, but two additional representatives of the Gondwanan relict group were also examined, and also head structures of Enicocephalidae, a member of a potentially basal heteropteran lineage. Features were compared to those documented in literature for the Sternorrhyncha, Auchenorrhyncha, and Heteroptera. Coleorrhyncha are characterized by highly modified head structures and correspondingly an entire series of autapomorphies, such as for instance a strongly flattened head capsule with fenestrations. However, they also display features that are likely plesiomorphic compared to members of other hemipteran groups. These include the almost complete tentorium and the lack of the gula. The sistergroup relationship between Coleorrhyncha and Heteroptera is well supported by cephalic features. Potential synapomorphies are the presence of a distinct mandibular sulcus, the reduced number of antennomeres, the absence of clasping organs in the labial groove, coiled accessory salivary ducts, the presence of a small cervical muscle M1a (M. pronotopostoccipitalis medialis), the presence of a second mandibular promotor M14 (M. zygomaticus mandibulae), the presence of M28 (M. verticopharyngalis), and M30 (M. frontobuccalis posterior).

1. Introduction

Coleorrhyncha is a highly aberrant group of insects and a key-taxon for the higher-level systematics of Hemiptera. It is represented by only a single recent family, the Gondwanan relict Peloridiidae (e.g. Schlee, 1969; Austin et al., 2004; Grimaldi and Engel, 2005; Schaefer, 2009), but the fossil record suggests that this taxon was once much more diverse. The oldest fossils unambiguously classified as Coleorrhyncha are the Late Jurassic and Early Cretaceous Laurasian Karabasiidae and the Early Cretaceous Hoploridiinae (Peloridiidae) from Transbaikalia (Popov and Shcherbakov, 1996). They show that the group was originally Pangean, with only few Southern Hemisphere species persisting until today. Much older fossils, the Late Permian to Early Cretaceous Progonocimicidae that once were widely distributed in Laurasia (e.g. Popov and Shcherbakov, 1991; Heads, 2008; Wang et al., 2009; Szwedo, 2011; Dong et al., 2012) have been classified as Coleorrhyncha (Popov and Shcherbakov, 1996), but are now tentatively considered as possible stem-group representatives of that clade (Grimaldi and Engel, 2005). Coleorrhyncha are undoubtedly one of the oldest groups of Hemiptera and represent an ancient lineage that has changed very little since Jurassic times (Pendergrast, 1962; Gullan and Cranston, 2005; Burckhardt, 2010).

Extant Peloridiidae include 17 genera and 36 species (Larivière et al., 2011). They occur in Southeastern Australia, New Caledonia, Southern South America (Evans, 1981; Burckhardt, 2009, 2010), and with the biodiversity hotspot in New Zealand (Larivière et al., 2011). Peloridiidae are found in temperate and subantarctic rainforests, especially those dominated by *Nothofagus* (Nothofagaceae) (Burckhardt, 2010; Burckhardt et al., 2011), although some species also occur in regions where the southern beeches are lacking (Carter, 1950). Both, habitus and life style, of peloridiids are cryptic and they are best collected from wet moss, hepatics and leaf litter using Winkler extractors (Burckhardt, 2010; Larivière et al., 2011). Their size ranges between two and five millimeters (Burckhardt

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and Agosti, 1991; Burckhardt, 2010). Most species are brownish, and almost all are covered with self-made incrustations of excretions blended with soil particles (Burckhardt, 2010). There are several records concerning bryophyte species harbouring peloridiids (summarized in Burckhardt, 2010). For *Hackeriella veitchi*, Helmsing and China (1937) recorded an association with the moss species *Papillaria kermadecensis* (now *P. crocea* (Hampe) A. Jaeger), but this was not confirmed in a recent field study (V. Hartung, unpublished data). Recent investigations into the biology of peloridiids have revealed that they can produce sounds (Hoch et al., 2006) and that they are able to jump (Burrows et al., 2007). Well known is the occurrence of endosymbiotic bacteria which are located in mycetomes one each side of the abdomen (e.g. Pendergrast, 1962; Schlee, 1969). They are typical for phytophagous Hemiptera (Larivière et al., 2011).

The phylogenetic position of Coleorrhyncha has been discussed controversially. Initially the group was placed close to the aquatic heteropteran family Ochteridae (Breddin, 1897). Coleorrhyncha were later treated as part of the "Homoptera" and ranked equivalent to the Sternorrhyncha and Auchenorrhyncha (e.g. Myers and China, 1929; Evans, 1937, 1957, 1963; Singh, 1971). Based on phylogenetic evaluation of morphological evidence across Hemiptera, Schlee (1969) found several synapomorphies for Coleorrhyncha and Heteroptera and concluded that they likely represent sister taxa. Subsequently, molecular evidence for this sistergroup relationship started to emerge (Wheeler et al., 1993; Ouvrard et al., 2000; Bourgoin and Campbell, 2002). The clade comprising Coleorrhyncha + Heteroptera (=Heteropterodea [or Prosorrhyncha; Sorensen et al., 1995; Schaefer, 2009]) is also strongly supported by the first multi-gene analysis with comprehensive taxon sampling of Hemiptera (Cryan and Urban, 2012) that also showed Auchenorrhyncha to be monophyletic. Building on this framework, studies focussing on the morphology of the enigmatic, species-poor and relictual Coleorrhyncha now have the potential to test hypotheses on character evolution that gave rise to one of the speciose and diverse clades among Hemiptera, the Heteroptera.

Head morphology has played an important role in investigating relationships among Hemiptera (e.g. Evans, 1937; Rieger, 1976; Hamilton, 1981). However, Rieger (1976) stressed that the poor documentation of the coleorrhynchan head leaves central homology hypotheses untested and negatively impacts systematic interpretations. Available descriptions of external and internal head structures of Peloridiidae are clearly incomplete. Line drawings of external head views have been published for several species including *Peloridium hammoniorum* (Popov and Shcherbakov, 1991), *Hemiodoecus leai* (frontal and occipital view: Myers and China, 1929; anterior portion of the adult head: Evans, 1981), and *Hemiodoecus fidelis* (Evans, 1937; Snodgrass, 1938). Ventral head structures and the tentorium of *Hemiodoecus* sp. were depicted by Hamilton (1981) and parts of the ventral head capsule, labial sensilla and internal structures of the feeding tube of *Xenophyes cascus* were treated by Brozek (2007), Burrows et al. (2007) and Burckhardt (2009). The most detailed study on internal structures of Peloridiidae was carried out by Pendergrast (1962). Nevertheless, this documentation of the inner structures of the head is very fragmentary consisting only of images of two cross sections of the head of *X. cascus* (muscles were marked, but not labelled and described in detail). A more comprehensive traditional treatment of the cephalic musculature was presented by Singh (1971) for *H. leai*.

The present study will fill the gap by providing the first detailed and well documented account of all external and internal head structures (including tentorium, muscles, nervous system and alimentary organs) of a species of Coleorrhyncha. Adults of *Hackeriella veitchi* were used for the anatomical investigation, as sufficient and appropriately preserved specimens were only available of this species. The results are compared with external features of two other species of Peloridiidae: *Peloridium hammoniorum* and *Pantinia darwinii*. *Pantinia* and *Peloridium* are closely related to each other and both occur in South America (Popov and Shcherbakov, 1996; Burckhardt, 2009), whereas *H. veitchi* is restricted to Australia (Burckhardt, 2009). The macropterous forms of *P. hammoniorum* (both sexes) are of special interest since they are the largest of all known peloridiids (Evans, 1981). An important plesiomorphic feature maintained in this species is the capacity to fly (Burckhardt, 2009), which is lacking in all other known members of the group. For comparison, the head anatomy of a species of the heteropteran Enicocephalidae (*Systelloderes* sp.) was studied in detail. Enicocephalomorpha are possibly the sistergroup of the remaining Heteroptera (e.g., Wheeler et al., 1993; Weirauch and Schuh, 2011), even though a basal position of Nepomorpha was suggested in a recent study (Li et al., 2012). A formal numerical character analysis is not presented here. It will be carried out in a subsequent study when more detailed data on hemipteran cephalic structures are available.

2. Material and techniques

2.1. Material

The present study is based on the following specimens:

Hackeriella veitchi (Hacker, 1932), two females, Queensland/Australia, Springbrook National Park, Repeater Station, 2006, leg. Geoff Monteith
Peloridium hammoniorum Breddin, 1897, one specimen (from N.P. Kristensen, Zoologisk Museum, Copenhagen)
Pantinia darwinii, China 1962, one specimen, Chile: IX Reg. Pr. Malleco, PNNahuelbuta, Administración, 37°50′S 73°00′W 1100 m, 23.12.1992, D. Burckhardt # 30b, det. D. Burckhardt 2009.
Systelloderes sp. (Enicocephalidae, Enicocephalomorpha), Peru: Cuzco: Wayqecha Research Center, 2821 m, 13°10′22″S 71°35′32″W, 05.12.2011, leg. C. Weirauch, P11L57 sweep/beat

Specimens of *H. veitchi*, *P. hammoniorum* and *Systelloderes* sp. were preserved in 70% ethanol. *P. darwinii* was air-dried. In the following text all species will be referred to by generic name only.

2.2. Scanning electron microscopy

Scanning electron (SEM) micrographs of *Hackeriella* and *Pantinia* were taken with a Philips XL 30 ESEM (FEI Company, Oregon, USA) and Scandium 5.0 Software (Soft Imaging System GmbH, Münster, Germany). *Hackeriella* was completely hydrated (distilled water) over several stages and macerated in 10% KOH for 24 h at 25 °C to remove soil particles. Additionally, the specimen was cleaned twice in a Bandelin Sonorex ultrasonic bath (BANDELIN electronic, Berlin, Germany) for two seconds each time. The KOH was washed out one hour in distilled water. Subsequently, it was completely dehydrated with ethanol (100%) over several stages and dried at the critical point (EmiTech K850, Quorum Technologies, West Sussex, UK). *Pantinia* was air-dried. *Hackeriella* and *Pantinia* were sputter-coated with gold (EmiTech K500, Quorum Technologies, West Sussex, UK). A rotatable specimen holder was used to mount the samples (see Pohl, 2010). After scanning the entire specimen, *Hackeriella* was partly re-hydrated (70% ethanol) and its head was removed. After complete dehydration with ethanol (100%) over several stages, it was dried at the critical point, sputter-coated with gold and fixed on the specimen holder for scanning of cephalic details.

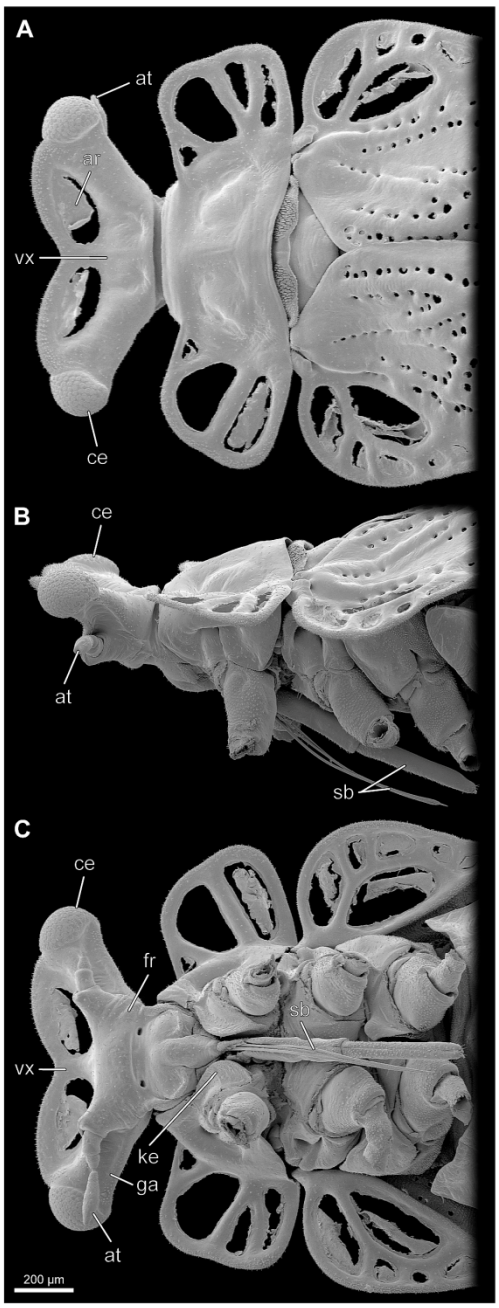

Fig. 1. *Hackeriella veitchi*, head and thorax, legs partly omitted; holes in areolae, paranota and wings are artifacts caused during specimen fixation, left antenna damaged. Scanning Electron Microscopy mircrograph (SEM). A: dorsal view; B: lateral view; C: ventral view. ar, areolae; at, antenna; ce, compound eye; fr, frons; ga, genal area; ke, prothoracic katepisterna; sb, suctorial beak, vx, vertex.

2.3. Cross-section series and 3D-reconstruction

One specimen of *Hackeriella* and one of *Systelloderes* were embedded in Araldite® (Huntsman Advanced Materials, Bergkamen, Germany) for semi-thin cross sectioning (1 µm) with a glass knife on a microtom HM 360 (Microm, Walldorf, Germany). The sections were stained with toluidine-blue. Images of sections for 3D-reconstruction of *Hackeriella* were taken with a Zeiss Axioplan (Zeiss, Göttingen, Germany), the AnalySIS® documentation system (Soft Imaging System GmbH, Münster, Germany) and a pixelink CCD-camera (PixeLINK, Ottawa, Canada). Figures were processed in Adobe® Photoshop® CS2 Version 9.0 (Adobe Systems Incorporated San Jose, California, USA) and Adobe® Illustrator® CS2 12.0.0 (Adobe Systems Incorporated, San Jose, California, USA). Alignment and three-dimensional reconstructions were done with Mercury Amira® 4.1.2 (Visage Imaging GmbH, Berlin, Germany) and surfaces were smoothed with Autodesk Maya® 7.0 (Autodesk GmbH, Munich, Germany).

2.4. Macro photography

Photographs of *Peloridium* (preserved in 70% ethanol, mounted on a microscope with a concavity) were taken with a Nikon D 90 digital SLR (Nikon Corporation, Tokyo, Japan), 16 or 25 mm Zeiss Luminar macro lenses (Zeiss, Goettingen, Germany), and adjustable extension bellows. The specimens were illuminated by two flashlights fitted with a transparent cylinder for even and soft light. Helicon Focus Mac Pro X64 (Helicon Soft Ltd, Kharkov, Ukraine) was used to combine several partially focused images to one completely focused image.

2.5. Terminology

The terms dorsal, ventral, anterior and posterior consistently refer to the longitudinal body axis (e.g., vertex dorsal, labium ventral). Muscles are continuously numbered in order of appearance. Subsequently a homologisation with the terminology of von Kéler (1963), Friedrich and Beutel (2008), and Wipfler et al. (2011) is suggested. The definition of ridges and sutures is following Wipfler et al. (2011).

3. Results

3.1. H. veitchi

The head structures are treated in a morphology based sequence starting with the head capsule, followed by the appendages, and finally the digestive tract, elements of the cephalic nervous system and glands. The muscles belonging to these structures are treated in the corresponding subsections.

3.1.1. Head capsule

The strongly flattened head is subtriangular with rounded edges and the ocular region strongly protruding anterolaterally (Fig. 1). It is sclerotised but the endocuticle is about four times thicker than the exocuticle (Fig. 10). The postoccipital region is partly retracted into the prothorax (Fig. 1). Due to the hypognathous condition, i.e. the posterior orientation of the mouthparts, the anterior head capsule is tilted, with the frons (fr) located on the ventral side (Fig. 1). In lateral view two distinct parts can be distinguished: the flattened and depressed anterior part including the vertex (vx),

genal area (ga) and compound eyes (ce), and a posterior cuboid part with the bases of the antennae, the mouthparts and the frons (Figs. 1 and 3A).

The flattened vertex (Fig. 1C) is anteriorly delimited by two strongly convex edges which meet medially ("anterior rims" of Burckhardt et al., 2011). The compound eyes (ce) are positioned at its lateral edges and are globular (Fig. 1A and B). Short sensilla are irregularly distributed between the ommatidia (Fig. 3A). The circumocular ridge is only weakly developed (Fig. 10B). Ocelli are absent. Within the ventral and dorsal parts of the vertex two oval semi-transparent fenestrations, areolae (ar) are formed by very thin two-layered cuticle (Figs. 1 and 10B). Mesally they are separated by a bridge ("median rim" of Burckhardt et al., 2011). The postero-ventral region of the cranial part of the head capsule between the

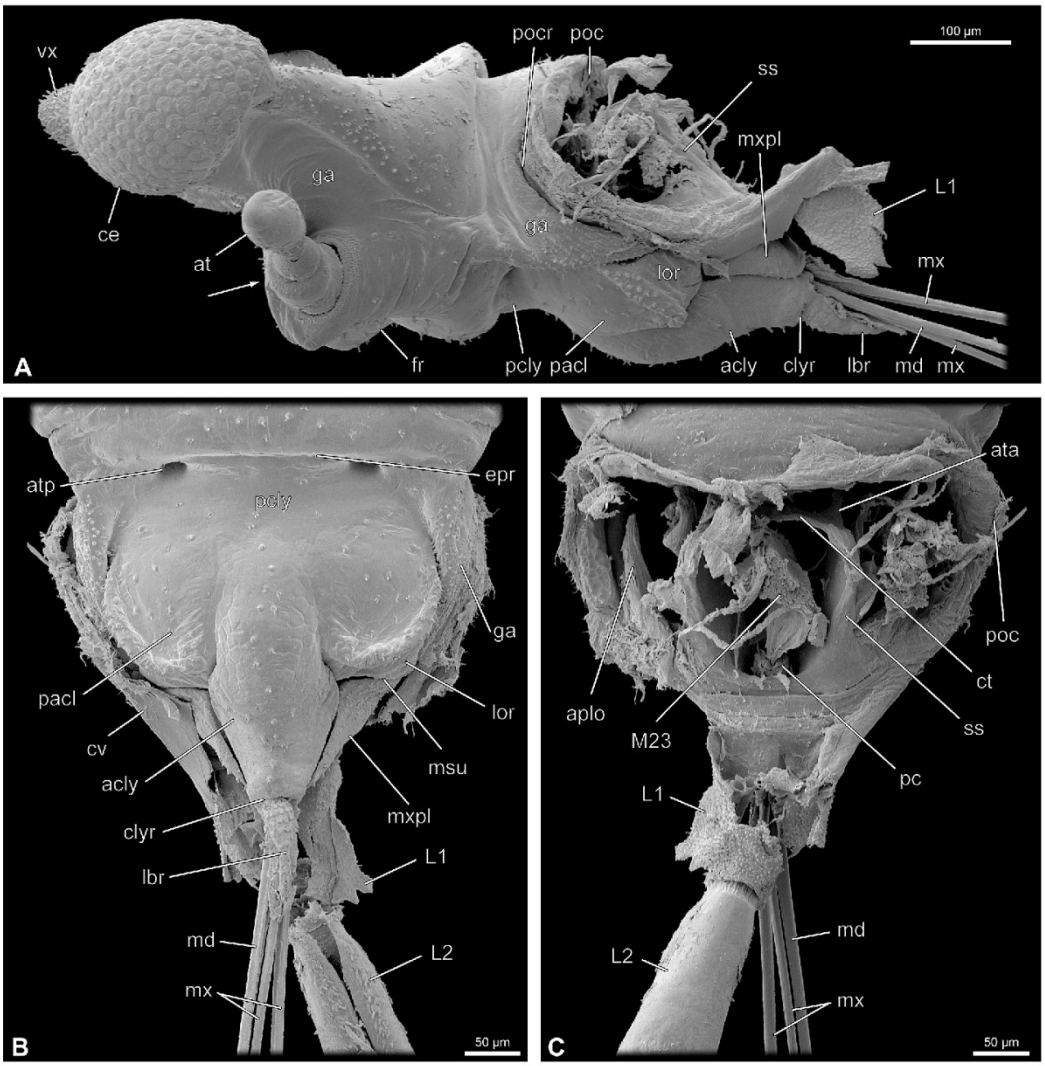

Fig. 2. *Hackeriella veitchi*, head, removed from thorax. SEM. A: lateral view, labium omitted, suctorial beak is not shown in full length; B: clypeus and labrum, ventral view; C: foramen occipitale with tentorium, dorsal view. acly, anteclypeus; aplo, apodeme of lorum/mandibular plate; at, antenna; ata, anterior tentorial arm; atp, anterior tentorial pit; ce, compound eye; clyr, clypeolabral ridge; ct, corpotentorium; cv, cervix; epr, epistomal ridge; fr, frons; ga, genal area; L1/L2, segment 1 and 2 of the labium; lbr, labrum; lor, lorum/mandibular plate; M, muscle with appropriate number (number of muscle corresponds to number in text, Figs. 9–12 and Table 1); md, mandible; mx, maxilla; msu, mandibular sulcus of Singh (1971); mxpl, maxillary plate; pacl, paraclypeal lobe of Singh (1971); pc, pumping chamber; pcly, postclypeus; poc, postocciput; pocr, postoccipital ridge; ss, suspensorial sclerite; vx, vertex. Arrow indicates edge which subdivides the head capsule (see Chapter 3.1).

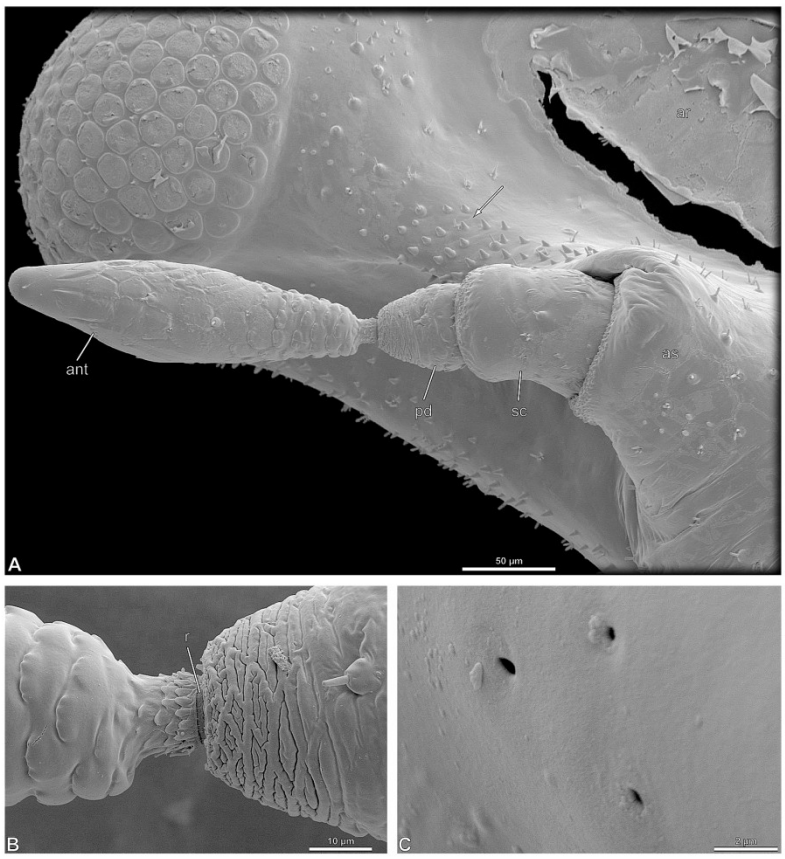

Fig. 3. *Hackeriella veitchi*, SEM. A: antenna, ventral view; B: passage from pedicellus to antennomere, ventral view; C: tip of antennomere, lateral view. ant, antennomere; ar, areolae; as, antennal socket; pd, pedicellus; r, ring-like structure; sc, scapus. Arrow indicates ridge, which is densely covered with thorns and short sensilla (see Chapter 3.1).

bases of the antennae and the compound eyes is formed by the genal area (ga) (Figs. 1 and 2). It is separated from the areolae by a distinct ridge (Fig. 1B), which is densely covered with thorns and short sensilla caudally (Fig. 3A, indicated by an arrow).

Close to the posterior margin of the areolae (Fig. 2A) a distinct edge sharply separates the flat anterior part of the head capsule from the posterior cuboid part (Fig. 2A, indicated by an arrow). The antennal bases are located on the anterior region, slightly postero-ventrad to the compound eyes. The slightly concave frons attaches posteriorly (Fig. 1C). Its separation from the ventral part of the vertex is not distinct. However, the aforementioned edge serves as a landmark. A well-developed epistomal ridge (epr) and the two deep invaginations representing the anterior tentorial pits (atp) separate the frons from the more posterior clypeus (Fig. 2B).

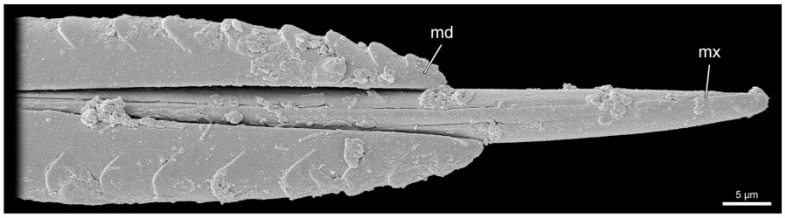

Fig. 4. *Hackeriella veitchi*, distal end of suctorial beak, SEM. md, mandible; mx, maxilla.

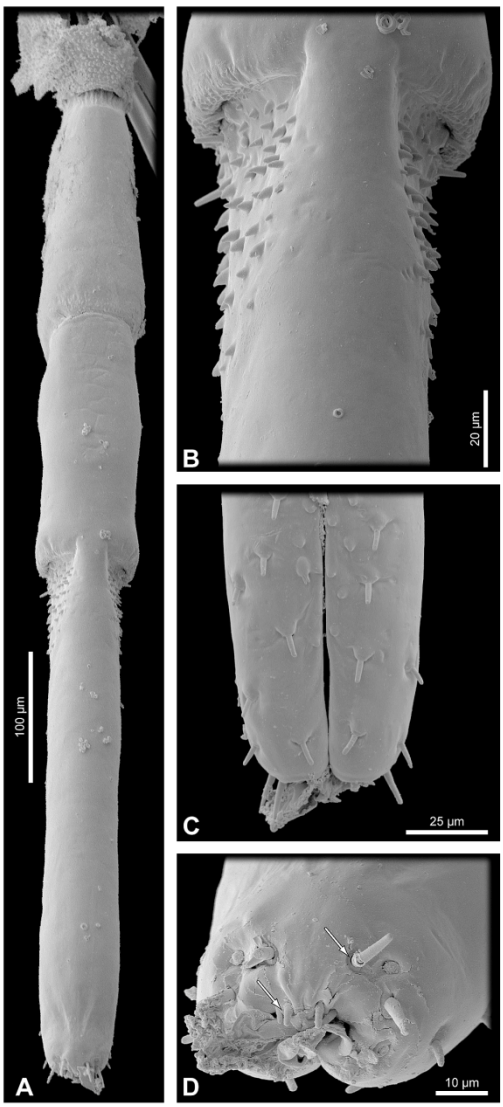

Fig. 5. *Hackeriella veitchi*, SEM. A: four-segmented labium, dorsal view; B: passage from third to fourth segment, dorsal view; C: tip of the fourth segment, ventral view; D: tip of the fourth segment, semilateral view, upper arrow indicates outer ring of sensilla, lower one inner ring of sensilla (compare with Fig. 6E).

Subgenal ridges as well as frontal and coronal (=epicranial) sutures are not distinguishable.

The edge of the large and triangular foramen occipitale is formed by a smooth, bulging postocciput without any protrusions. It is separated from the posterior genal regions by the postoccipital ridge (pocr) (Fig. 2A and C).

Musculature (M1–M3). M1 (Figs. 11A and 12B): O (=origin) – laterally on the pronotum; I (=insertion) – dorsolaterally at the postocciput; F (=function) – levator of the head (simultaneous contraction of both partitions of this paired muscle) or rotator. M1a (Figs. 10F and 11B; muscles with a small letter are treated as a separate and discrete unit): O – pronotum, near the dorsal vessel; I – dorsomedially on the postocciput; F – retractor of the head. M2 (Fig. 11B): O – mesonotum; I – dorsomedially on the postocciput; F – levator of the head. M3 (Fig. 11A): O – mesal region of the pronotum; I – apodeme of the maxillary plate (apmp; Fig. 12B); F – unclear.

3.1.2. Endoskeleton

The well developed tentorium comprises anterior arms, posterior arms, and a corpotentorium, whereas the dorsal arms are absent (Figs. 11A and 12B). The slender anterior tentorial arms (ata) extend from the distinct anterior tentorial pits (atp) to the flattened corpotentorium (ct), a nearly rectangular plate (Figs. 2B, 10E and 11A). The short and stout posterior arms (pta) are connected to the posterior side of the corpotentorium (Fig. 12A and B). The minute posterior tentorial pits (ptp) are located in the fold between the maxillary plates (mxpl) and occiput, just anterad the fusion of the apodeme of the maxillary plate (apmp) with the suspensorial sclerite (Fig. 10G).

Additional endoskeletal elements are the more ventrally located hypopharyngeal wings, and the piston of the salivary pump. The latter are described in the chapter "*Hypopharynx, salivary pump and salivary glands*".

Musculature (M4–M5a). M4 (Figs. 10G and 11A): large and compact muscle, O – pronotum, attachment area visible externally as two indentations (Fig. 1A); I – posterior part of the posterior tentorial arm; F – depressor of the head. M5 (Figs. 10H and 11A): O – anterior region of the profurcal arms (fap), posterad the base of the basal labial segment; I – posterior tentorium or border region of suspensorial sclerites and head capsule; F – levator and retractor of the head. M5a (Figs. 10H and 12B): long and slender, unpaired, only present on the left side of the body (but probably an artifact; not immediately associated with the tentorium but very close to M5), O – anterior region of the left profurcal arm; I – dorsal region of the apodeme of the maxillary plate (apmp); F – unclear.

3.1.3. Clypeus, mandibular and maxillary plates and labrum

The small convex labrum (lbr) is elongate triangular and appears almost tongue-shaped. It is separated from the clypeus by the clypeolabral ridge (clyr) (Fig. 2A and B). The basal region of the labrum is covered with plate-like, caudally directed tubercles. The labrum forms the dorsal closure of the base of the feeding tube.

The tripartite clypeus is formed by a flattened postclypeus (pcly) directly posterad the epistomal ridge, an elongated and convex median anteclypeus (acly), and two paraclypeal lobes (pacl) laterad the latter structure (Fig. 2A and B). The dorsal side of the anteclypeus is clearly separated from the remaining clypeus by an incision and bears the opening of the prepharynx (pph) (Fig. 12A). A slender, V-shaped apodeme with a bifurcated apex (apph) originates at the base of the anteclypeus. It is directed craniodorsad and covers the dorsolateral sides of the prepharynx (Figs. 10F and 12A).

The maxillary stipital lobes or maxillary plates (mxpl, see Snodgrass, 1938) are located laterad to the anteclypeus (Fig. 2A and B). They are tapering caudally and end at the distal part of the anteclypeus, proximad the labrum. The lateral side of the maxillary plate forms a flattened apodeme (apmp) internally, which is fused with the transition region of the suspensorial sclerite to the head capsule posterad (Figs. 9 and 10G). The mesal area of the maxillary plates, the hypopharynx and the anteclypeus form a guiding device for the stylets (Fig. 9A). The Evans' organ ("organe d'Evans" in *H. leai* China of Bourgoin, 1986a) is not distinguishable.

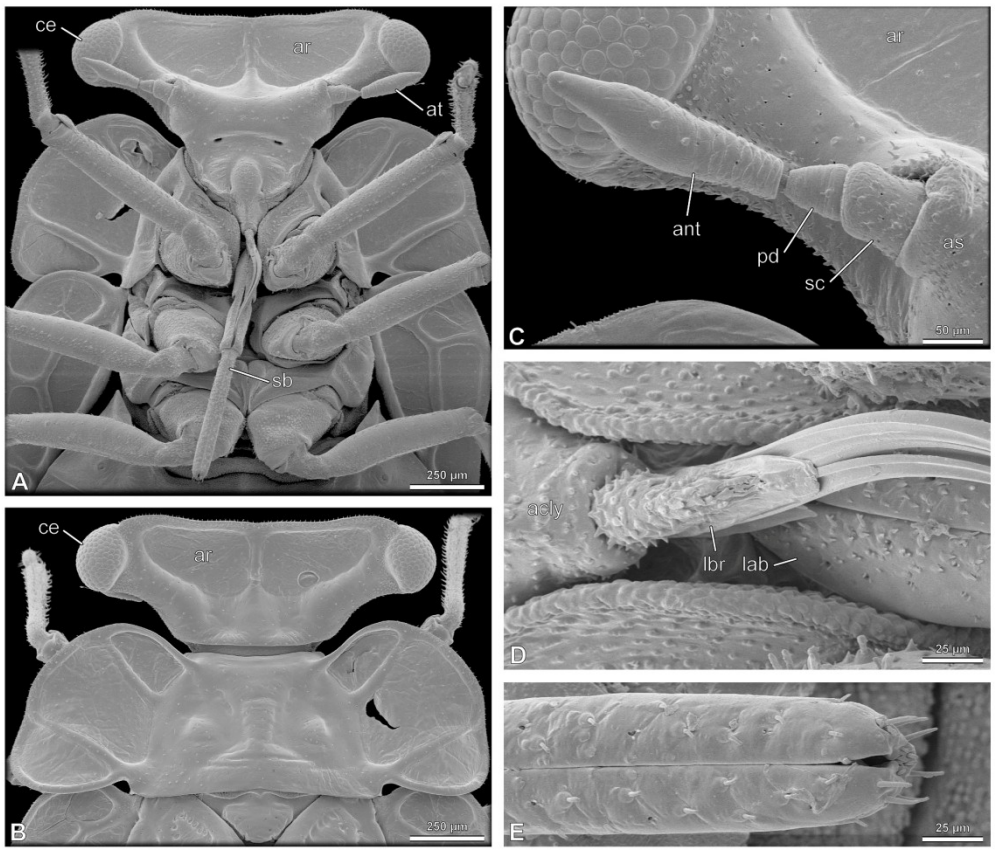

Fig. 6. *Pantinia darwini*. SEM. A: head and thorax, ventral view; B: head and thorax (partly) dorsal view; C: antenna, ventral view; D: labrum, ventral view; E: distal end of labium, ventral view (one sensillum of the outer ring broken off). acly, anteclypeus; ant, antennomere; ar, areolae; as, antennal socket; at, antenna; ce, compound eye; lab, labium; lbr, labrum; pd, pedicellus; sb, suctorial beak; sc, scapus.

The lora (lor) or mandibular plates (according to Matsuda (1965) a term without "precise morphological meaning"; see also Singh, 1971; Strümpel, 2010) are crescent-shaped and fused with the paraclypeal lobes (Fig. 2B). A curved bulge with sensilla is situated between the lorum and paraclypeal lobe. Internally the mandibular plate forms a distinct cresent-shaped apodeme (aplo) (Figs. 2C, 10F and 12B).

Laterad to the lorum an extension of the genal area (ga) is present as a convex sclerite, which is partly covered by the paraclypeal lobe. The membranes attached to this genal area are likely a part of the cervix (cv) (Fig. 2B). The genae are separated from the lora and the maxillary plates by the mandibular sulcus (msu) (see Singh, 1971) (Fig. 2B). Only very few sensilla are inserted on the clypeal surface. Labrum, labium and anteclypeus form a tunnel-shaped device containing the mandibular and maxillary stylets (Figs. 1C and 11A).

Musculature (M10–M11). No muscles are associated with the labrum. M10 (Figs. 10F,G and 11B): two bundles, O – pronotum, proximad the origin of M3; I – lateral region of the prothorax, anterad the apodeme of the lorum/mandibular plate; F – unclear. M11 (Figs. 10D,E and 11A): three bundles, O – apodeme of the lorum/mandibular plate; I – postclypeus; F – unclear.

3.1.4. Antennae

The three-segmented antennae are inserted on a prominent antennal socket (as), postero-ventrad to the compound eyes (Fig. 3A). The circumantennal ridge is distinct (Figs. 2A and 3A). An antennifer is absent. The scapus (sc) is cylindrical, slightly bent caudad, and two times longer than the pedicellus (pd) (Figs. 2A and 3A). The pedicellus tapers distally to one third of its basal width. Distinct cuticular folds characterize the distal half of the pedicellus (Fig. 3B). The ventral and dorsal sides of the scapo-pedicellar region are both characterized by a more or less distinct strand of nuclei of the nerval connective tissue (nct) (Fig. 10B). The flagellomere is formed of a single spindle-shaped antennomere (ant). Its proximal end is stalked and its surface structure resembles that of a pine cone (Fig. 3B). On the caudal side of its tip seven pits are present (three are visible in Fig. 3C). Between the flagellomere and the pedicellus, a slender, ring-like structure (r) is visible on the SEM micrograph (Fig. 3B), but not distinguishable in the cross section

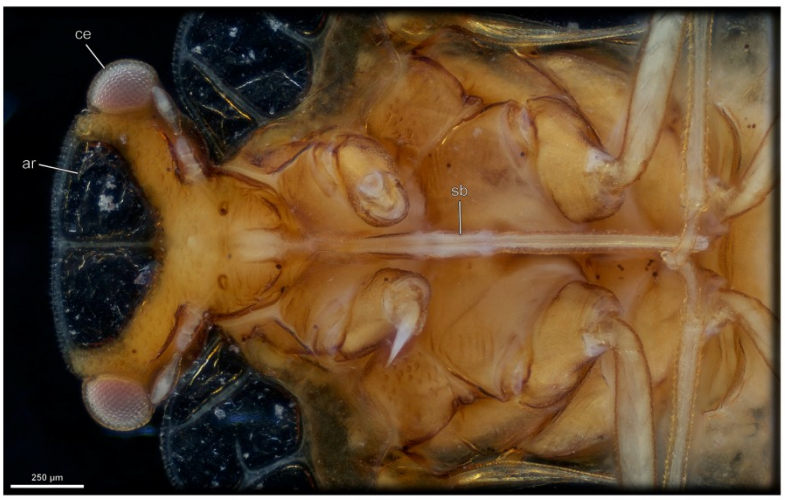

Fig. 7. *Peloridium hammoniorum*, head and thorax, first pair of legs partly omitted, ventral view, microphotograph. ar, areolae; ce, compound eye; sb, suctorial beak.

(Fig. 10B). All regions of the antennae bear an irregular and sparse vestiture of sensilla. Antennal hearts and associated muscles are not recognizable and apparently absent.

Musculature. Extrinsic and intrinsic antennal muscles (M6–M9). M6 (Figs. 10C and 11A): O – anterior tentorial arm; I – posterad the ventral base of the scapus; F – depressor of the antenna. M7 (Figs. 10C and 11A): O – anterior tentorial arm, close to the anterior tentorial pit; I – dorsally on the base of the scapus; F – levator of the antenna. M8 (Figs. 10B and 12B): O – ventral base of the scapus; I – dorsal base of the pedicellus; F – extensor of the pedicellus. M9 (Figs. 10B and 12B): O – ventral base of the scapus, proximad M8; I – ventral base of the pedicellus; F – flexor of the pedicellus.

3.1.5. Mandible

The mandibles (md) are a pair of slender, ventro-caudally directed stylets, which are articulated within the head capsule. The basal part is plate-like, whereas the caudal part is transformed into a funnel (Figs. 10D,F and 11B). The transition area between the basal part to the funnel-like part is surrounded by delicate membranes. However, a distinct mandibular sac is absent. The protractor muscles of the mandible insert directly at the plate-like region. A mandibular lever is missing. Close to the labral base, each of the mandibular stylets form a spur, which is directed inwards and mechanically supports the enclosure of the smaller maxilla (Fig. 9C). The mandibular apices almost reach the metacoxae posteriorly (Fig. 1B and C). The external surface of the stylets is largely glabrous, but distinct cuticular scales are present on the distal region (Fig. 4). Mandibular glands are absent.

Musculature. Retractor and promotors of the mandibular stylet (M12–M14). M12 (Figs. 10C and 11A): three large bundles, O – mesal region of the roof of the head capsule; I – short tendon at the dorsal and proximal outer edge of the plate-like mandibular base; F – retractor of the mandibular stylets. M13 (Figs. 10D and 11A): stout muscle, O – anterior tentorial arm; I – mesal side of the plate-like region; F – promotor of the mandibular stylets. M14 (Figs. 10D and 11A): stout muscle, O – anterior tentorial arm; I – ventral anterior margin of the plate-like part; F – promotor of the mandibular stylets.

3.1.6. Maxilla

The maxillae (mx) are mainly represented by slender, ventro-caudally directed stylets, which are articulated within the head capsule. The maxillary base is a funnel-shaped sclerite with a thin layer of membrane wrapped around it. However, a distinct maxillary sac and a maxillary lever are not present (Figs. 10E, 11B and 12). The distal maxillary part tapers strongly. The external surface is devoid of scales (Fig. 4). The palp and galea are absent. The other elements appear indistinguishably fused, without a recognizable detachment of the lacinia from the stipes. At least the distal thirds of the stylets were very closely adjacent to each other in the examined specimen (Figs. 1C and 4). The stylets are about 30 µm longer than those formed by the mandibles and reach the metacoxae posteriorly (Fig. 1B and C). Maxillary glands are absent.

Musculature. Retractor and promotor of the maxillary stylet (M15, M16). M15 (Figs. 10D,E and 11B): two bundles, O – roof of the head capsule, near M12; I – dorsally on the basal part of the maxilla; F – retractor. M16 (Figs. 10F,G and 11B): O – outer wall of the suspensorial sclerite and outer wall of the maxillary plates; I – posteriorly on the basal part; F – promotor.

3.1.7. Labium

The tube-like, four-segmented and straight labium (lab) forms a sheath for the mandibles and the maxillae. This functional complex is called the "feeding tube" or "suctorial beak" (sb). It has a ventro-caudal orientation (Fig. 1B and C). The labial groove (lg) lies on the ventral[1] side of segments two to four (Fig. 13). The basal segment (L1) is directly attached to the ventral base of the postocciput (poc). It bears a dense vestiture of tubercles, and is partly covered by the two prothoracic katepisterna (ke) (Figs. 1C, 2C and 5A). The basal segment is less sclerotised than the distal ones. In contrast to the glabrous dorsal surfaces of the three distal segments, the ventral surfaces are densely covered with ventro-caudally directed sensilla and tubercles (Figs. 2B and 5A,C). The second segment (L2) is

[1] The terms dorsal and ventral refer to the position of the labium as seen in Fig. 1B.

Fig. 8. *Peloridium hammoniorum*, head. microphotograph. A: dorsal view; B: ventral view. ar, areolae; at, antenna; atp, anterior tentorial pits; ce, compound eye; oc, ocellus.

separated from the third (L3) by a distinct incision on the ventral side (Figs. 1C and 5A). The transition between both segments is marked by an indentation. The third segment is clearly separated from the fourth (L4) by an incision, which is interrupted dorsally by a longitudinal stripe of cuticle. The regions laterad to this stripe, which are at the same time the base of the apical segment, are covered with sensilla and tubercles (Fig. 5B). The fourth segment is about as long as the added up length of L2 + L3. The lateral sides of its base form two stout apodemes internally (apL4) (Fig. 13). Its tip is rounded and bears two almost circular rows of sensilla. The inner circle comprises four short conical sensilla, which are closely adjacent to each other. The outer ring is composed of eight longer sensilla (Fig. 5C and D).

Musculature. Extrinsic and intrinsic labial muscles (M17–M22). M17 (Figs. 10H, 11A and 12B): long and slender, O – posterior tentorial arm; I – posterior base of segment 2 (L2); F – retractor. M18 (Figs. 10H, 11A and 12B): long and slender, O – posterior tentorial arm, ventrad M17; I – anterior base of segment 2; F – retractor. M19 (Figs. 10H, 11A and 12B): smallest labial muscle, O – mesal base of segment 2; I – anterior base of segment 2, near M18; F – unclear. M20 (Fig. 11A): largest labial muscle, unpaired, O – anterior base of segment 2, at the labial groove; I – dorsal base of segment 3 (L3), near the origin of M21; F – unclear. M21 (Figs. 11A and 12B): O – lateral sides of proximal part of segment 3; I – laterally on the distal region of segment 3; F – unclear. M22 (Fig. 13): O – proximal half of dorsal side of segment 3; I – basal apodemes of segment 4 (apL4); F – unclear.

3.1.8. *Hypopharynx, salivary pump and salivary glands*

Two strongly sclerotised plates (hypopharyngeal wings or suspensorial sclerites, ss) are present laterad to the tentorium (Figs. 2C,

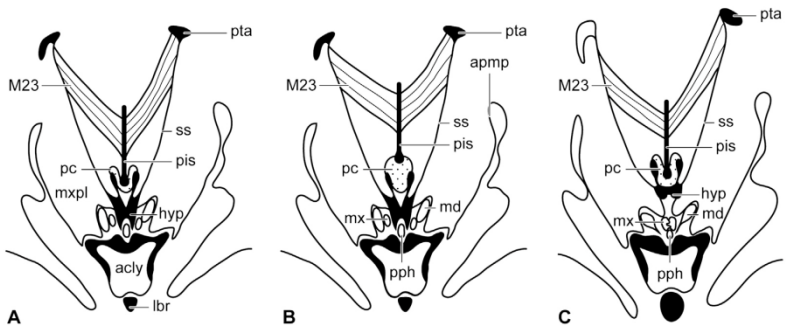

Fig. 9. *Hackeriella veitchi*, salivary pump, cross sections, schematic. A: relaxed condition; B: hypothesized active condition (for plane of section of A/B see Fig. 10G); C: relaxed condition (plane of section posterad A/B). acly, anteclypeus; apmp, apodeme of maxillary plate; lbr, labrum; hyp, hypopharynx; M, muscle with appropriate number (number of muscle corresponds to number in text, Figs. 10–12 and Table 1); md, mandible; mx, maxilla; mxpl, maxillary plate; pph, prepharynx; pc, pumping chamber; pis, piston; pta, posterior tentorial arms (anterad posterior tentorial pits).

9 and 10G). Their dorsal sides merge with the corpotentorium and the posterior arms (Figs. 11A and 12B) while their bases are fused with each other, but provided a gap for the salivary duct connecting the pumping chamber with the salivary channel of maxillae (sdmx) (Figs. 9 and 12A). The inner lateral sections of this funnel's base are characterized by two clamps, which partly enclose the lateral sides of the pumping chamber (Fig. 9). The posterior parts of the suspensorial sclerites merge with the head capsule (Fig. 12B). The hypopharynx (hyp) is associated with the ventral base of the fused suspensorial sclerites and located between the mandibular and maxillary stylets (Fig. 12A). Its bifurcated ventral side covers the anterior part of the prepharynx (Fig. 9A and B) and is also connected with the salivary pump. The entire functional complex comprises the suspensorial sclerites, the piston, the pumping chamber and the two muscles described below (Fig. 9). Between the suspensorial sclerites and below the corpotentorium, a wing-like free standing piston (pis) is present. Its posteroventral part is thickened and connected with the membranous pumping chamber (pc) (Figs. 9 and 11A). The salivary pump is dorsoventrally oriented. In *Hackeriella* two pairs of salivary glands are present. They are situated on both sides of the gut. The principal gland (sg1) is composed of two fused globular parts and located in the prothorax posterad to the suspensorial sclerites. It is not clearly separated in an anterior and posterior lobe. As it is attached to the first thoracic ganglion (ftg), the innervation with individual nerves is uncertain (Fig. 14B). The vesicular accessory gland (sg2) is more voluminous and extends from the meso- to the metathorax (Fig. 14A and C; see also Fig. 9 of Pendergrast (1962)). In contrast to the principal gland its innervation (nv) is distinctly recognizable and there are more nuclei (n) and secretory granules (se) than in sg1 (Fig. 14C). Both salivary glands are enclosed each by a thin tunica propria (tp).

The slender accessory ducts (sd2) reach the postoccipital region posteriorly, where they partly surround the dorsal part of the suspensorial sclerites and the posterior tentorial arms (Fig. 12B). In their further course the ducts make a turn posterad and join the shorter principal ducts (sd1). The stout common salivary duct (sd) of both glands merges with the pumping chamber (Fig. 14A). The different salivary ducts are very similar histologically. The common salivary duct is slightly thickened anterad. The transition of the salivary duct into the salivary channel and the transition of the gut into the food channel of the maxillae could not be reconstructed precisely with the available section series.

Musculature. M23 (Figs. 9–11A): one of the largest muscles of the head, O – mesal side of the suspensorial sclerites; I – piston connected with the pumping chamber; F – contraction results in an extension of the pumping chamber (pc) and influx of saliva from the salivary glands (Fig. 9B); relaxation pulls the piston into the pumping chamber and reduces its volume, thus pumping saliva through the maxillary salivary channel (Fig. 9A and C). M24 (Fig. 12A and B): O – postero-ventrad the origin of M23 at the mesal side of the suspensorial sclerites; I – anterio-dorsal side of the fused salivary ducts; F – probably support of M23.

3.1.9. Epipharynx

The epipharynx is not clearly distinguishable. It is apparently represented by a flat region on the caudal clypeal region.

Musculature. M25 (Figs. 10F and 12A): Y-shaped, O – postclypeus, posterad the origin of M26; I – cranial face of the precerebral pharynx, ventrad the insertion of M26; F – dilation of the pharynx.

3.1.10. Pharynx

Due to the hypognathous condition the cephalic foregut is distinctly bent near the occipital region (Fig. 12A). The lumen of the precerebral part in the occipital region (prepharynx) is distinctly narrower than that of the postcerebral part. The precerebral pharynx is characterized by minute sclerotised plates (sp) (Fig. 10F). The muscle layer is strongly reduced and only represented by few delicate fibres near the region of the corpotentorium.

Musculature. Pharyngeal muscles (M26–M30). Longitudinal muscles absent, ring musculature extremely reduced, only few fibres recognizable. M26 (Figs. 10F and 12A): one of the largest muscles, Y-shaped, O – postclypeus; I – cranial side of the cibarium; F – dilation of the cibarium, uptake of liquid food substrate via the food channel. M27 (Fig. 12A): V-shaped, O – postclypeus, anterad the origin of M26; I – precerebral pharynx, dorsad the insertion of M26; F – dilator. M28 (Fig. 12A): O – mesal region of the roof of the head capsule, close to the origin of M12; I – dorsal side of the pharynx, immediately posterior to the bend; F – dilator of the precerebral pharynx. M29 (Figs. 11A and 12B): O – anterior tentorial arm; I – laterally on the pharynx, close to the bend; F – stabilization of the pharynx during food uptake. M30 (Fig. 12A): unpaired, O – posterior part of the frons, I – pharynx near the tritocerebral region; F – dilator.

3.1.11. Brain

The cephalic part of the central nervous system forms a compact structural unit, with a narrow passage for the pharynx between the

brain and the subesophageal ganglion. The brain fills out large parts of the head capsule, especially in the anterior region (Fig. 12A). Proto-, deuto- and tritocerebrum are not clearly separated from each other externally. The protocerebral region is characterized by a high density of nuclei of the connective tissue (nct), whereas the neuropil (np) is less strongly developed. The optic lobes (oplo) are moderately sized (Figs. 10B and 12A). The density of nuclei of the connective tissue is strongly reduced in comparison to that of the central protocerebral region. Two posteriorly directed processes of the tritocerebrum are connected by a loose meshwork of nerve fibres (Fig. 12A). The very short and broad circumesophageal connectives (cpc) originate at the posterior tritocerebrum (Fig.12A). The subesophageal ganglion (sog) is located posterad the tritocerebral processes in the central occipital region. It is fused with the first thoracic ganglion (ftg) (Fig. 12A). The neuropil (np) of the circumesophageal connectives and of the subesophageal ganglion is less dense than in the brain. The thin neural lamella (nl) forms the outer cell layer of the cephalic nervous system. The neurilemma (nr) of the brain is not developed as a continuous layer, but only composed of few flattened cells (distinct in the subesophageal and frontal ganglion; Fig. 14B). The antennal, mandibular, maxillary, and labial nerves could not be reconstructed precisely with the available section series. The frontal ganglion is not recognizable as a separate structure (see also Fig. 23 of Pendergrast, 1962).

3.2. *P. darwini*

As the general external head morphology of *Pantinia* is very similar to that of *Hackeriella*, only differences will be described in the following. The anterior border of the areolae is less convex but nearly straight (Fig. 6A and B). In contrast to *Hackeriella*, the ventrolateral sides of the head (between the compound eye and the antennal socket) are perforated and densely covered with cranially directed triangular scales (Fig. 6C). The antenna (Fig. 6C) lacks a recognizable ring-like structure between the flagellomere and the pedicellus. The shape of the labrum and labium is very similar to the condition found in *Hackeriella* (Fig. 6A and D). The same bicircular arrangement of sensilla is present at the labial apex (Fig. 6E).

3.3. *P. hammoniorum*

The external head morphology is very similar to that of *Hackeriella* and *Pantinia*. However, paired ocelli (oc) are present between the evenly convex margin of the head and the compound eyes (Fig. 8A). A third inconspicuous ocellus is located on the ventral side in the middle of the frontal region (Fig. 8B). The antennae are similar to those of *Hackeriella* and *Pantinia* (Fig. 8B). The basal and distal regions of the third labial segment are strongly membranized as shown in Fig. 7.

4. Discussion

In the following, implications of the cephalic features of Coleorrhyncha will be discussed in the context of the phylogeny of Hemiptera, with the main focus on Heteropterodea (Heteroptera + Coleorrhyncha). In the subsections the characters will be discussed in a morphology based sequence, i.e. largely following the descriptive part of this study.

The cephalic muscle system is treated in a separate section of the discussion. As the presently available data for Auchenorrhyncha and Sternorrhyncha is very fragmentary, only a preliminary phylogenetic interpretation is presented. This part of the discussion is mainly focused on the homology of the head muscles.

4.1. Musculature

The cephalic musculature of *Hackeriella* is compared with conditions found in the peloridiid *H. leai* (Singh, 1971), in different heteropteran groups (*Ochterus marginatus* [Ochteridae, Nepomorpha] (Rieger, 1976); *Corixa punctata* [Corixidae, Nepomorpha] (Benwitz, 1956; Rieger, 1976); *Saldula pallipes* [Saldidae, Leptopodomorpha] (Parsons, 1962, 1963), *Systelloderes*), and in the aphid genus *Aphis* (Weber, 1928). Additionally, the muscles of *Hackeriella* are homologized with those listed in the nomenclatorial systems of von Kéler (1963), Friedrich and Beutel (2008), and Wipfler et al. (2011) (Table 1). The cephalic muscle system of the studied specimens of Coleorrhyncha is largely uniform. However, Singh (1971) described a muscle "3" responsible for the movement of the flagellomere of *Hemiodoecus*, originating at the base of the pedicellus and extending to the base of the apical antennomere. This muscle is absent in *Hackeriella*. It is conceivable that Singh (1971) misinterpreted the clustered nuclei of the nerval connective tissue as a separate muscle. The presumptive homologues of **M1** (Musculus cervicopostoccipitalis (von Kéler, 1963)), **M1a** (M. pronotopostoccipitalis medialis), **M5** (M. profurcatentorialis), **M5a** (M. profurcacervicalis) and **M10** (pronoto-loral apodeme muscle) were not identified by Singh (1971). As these muscles are localized in the cervical region or originate in the prothorax, it is conceivable that they were damaged or destroyed when the head was separated from the postcephalic body for dissection. The aquatic *Ochterus* (Ochteridae, Nepomorpha) (Rieger, 1976), presumably a relatively "basal" heteropteran representative, display a very similar set of muscles as it is present in Coleorrhyncha. In some cases the precise morphological condition appears ambiguous and is therefore discussed in more detail in the following.

M3 (pronotal muscle of the maxillary plate) and 52 of *Hemiodoecus* both insert on the apodeme of the maxillary plate. However, M3 has its origin on the pronotum, whereas 52 orginates on the prosternal apophyses in *Hemiodoecus*. The corresponding muscle in *Ochterus*, *Systelloderes*, and *Aphis* inserts at the lateral or ventrolateral postoccipital region. The assumed homology would imply a shift of the insertion posterad the maxillary plates in *Hackeriella*. The homology assessment of **M5** (M. profurcatentorialis) and similar muscles described for heteropterans and *Aphis* implies a shift of the insertion from the postoccipital processes to the dorsal part of the tentorium or border region of the tentorium and head capsule. Although maxillary glands are absent in Coleorrhyncha, **M5a** (M. profurcacervicalis) could be homologous to the dilator of the orifice in Heteroptera as the structure and insertion are congruent. This muscle is probably homologous to muscle 66 (M. profurcacervicalis) of von Kéler (1963) and Ivlm1 (M. profurcacervicalis) of Friedrich and Beutel (2008). Although it is similar in position this would imply a shift of the insertion to the cervical sclerites. According to Breider (1952) a maxillary gland also occurs in aphids, which suggests that the corresponding dilatator should be also developed. However, it was not mentioned in his study. In contrast to *Hackeriella* the homologues of **M6** (M. tentorioscapalis anterior) and **M7** (M. tentorioscapalis posterior) originate on the cranium in Heteroptera and not on the anterior tentorial arms, which are absent (see above). This shift is a derived condition correlated with the tentorial reduction and a possible heteropteran autapomorphy. **M10** (pronoto-loral apodeme muscle) of *Hackeriella*, TM11 (M. noto-pleuralis) of *Ochterus* and Idvm5 (M. pronoto-cervicalis anterior) of Friedrich and Beutel (2008) originate on the protergum. However, M10 inserts near the loral apodeme whereas TM11 is attached to the pleural region and Idvm5 on the posterior margin of the second lateral cervical sclerite. Apparently the homology is uncertain, but an anterior shift of the insertion site in *Hackeriella* could be due to the markedly

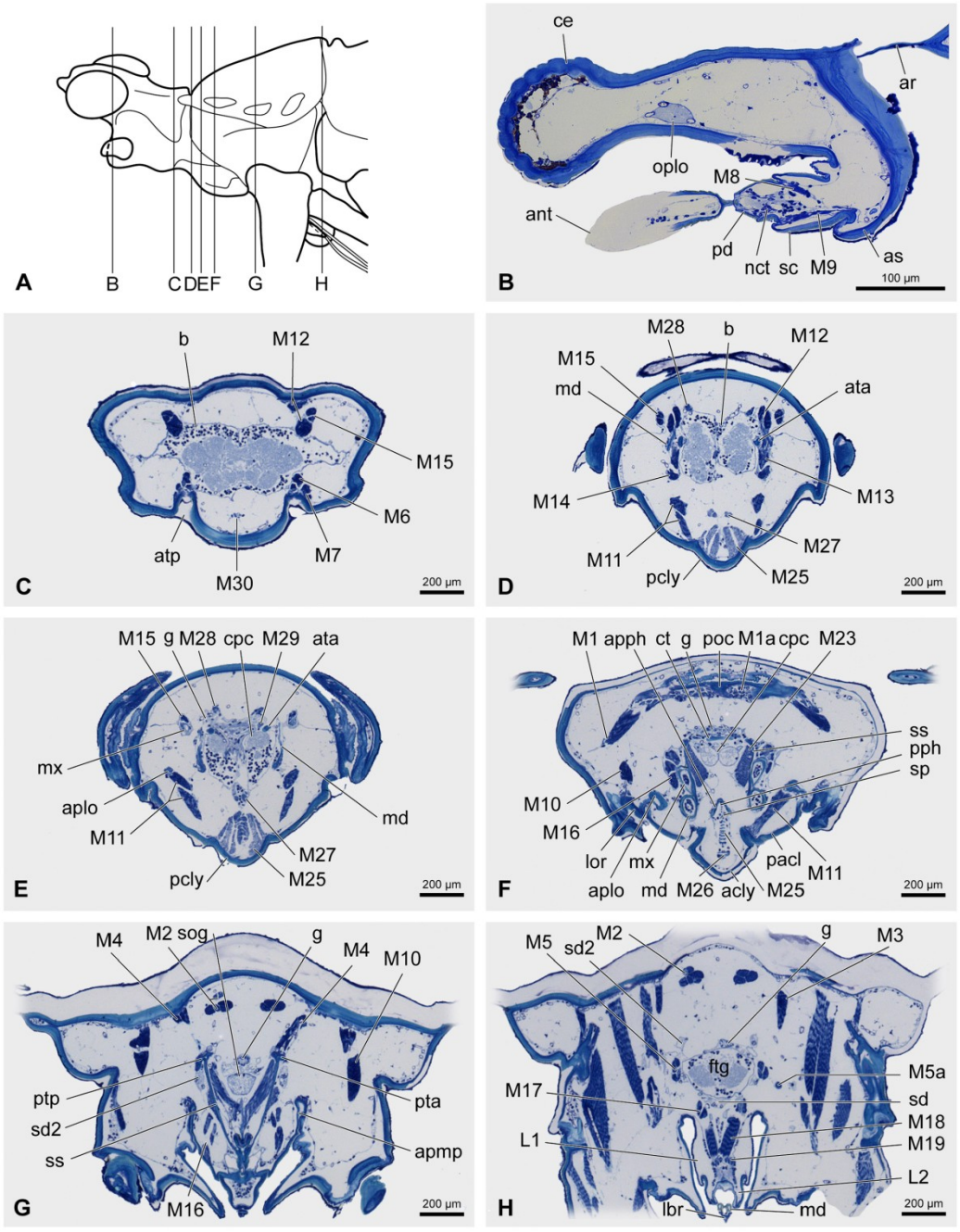

Fig. 10. *Hackeriella veitchi*, cross sections. A: head and thorax, schematic, lateral view showing planes of section of light micrographs B – H. B: only left part of head is shown, apical part of antennomere and connection to areolae damaged; G: for detailed lettering see Fig. 9A–B. acly, anteclypeus; ant, antennomere; aplo, apodeme of lorum/mandibular plate;

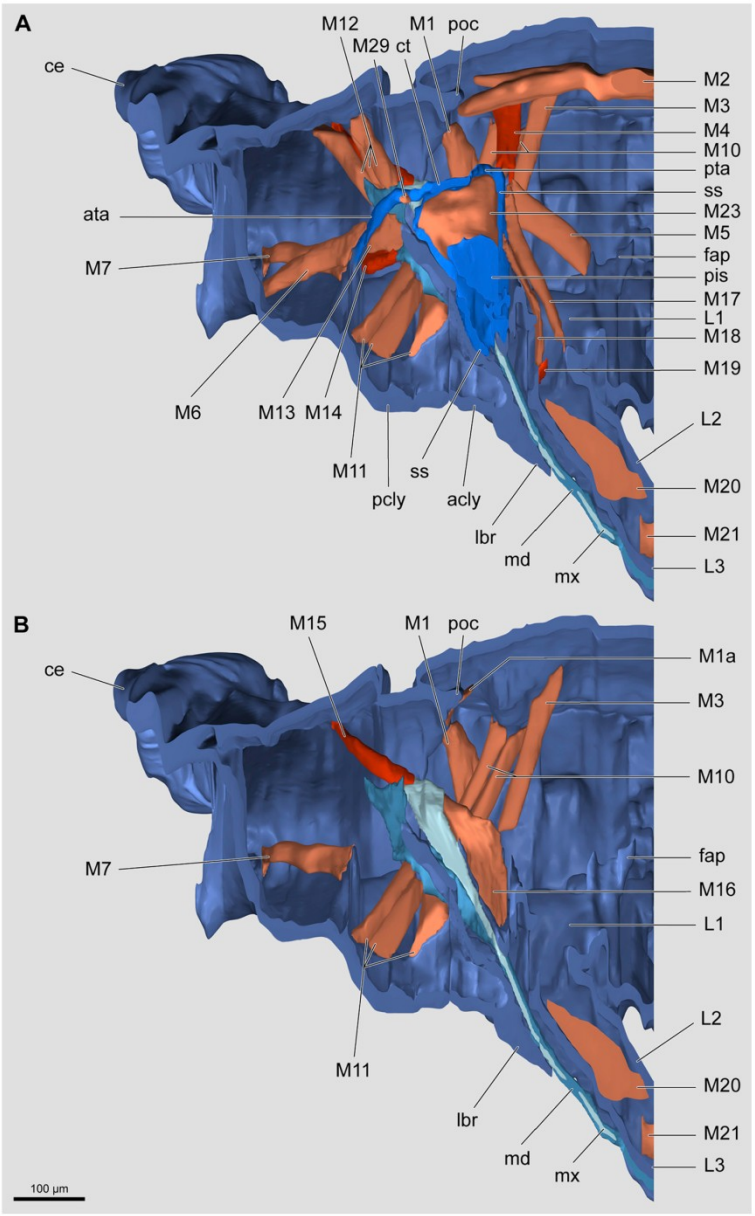

Fig. 11. *Hackeriella veitchi*, head and prothorax (legs omitted), 3D-reconstruction, sagittal section, different muscles shown, tentorium omitted in B (blue: sclerotization, red: musculature). Areolae and forehead slightly rammed during fixation. acly, anteclypeus; ata, anterior tentorial arm; ce, compound eye; ct, corpotentorium; fap, profurcal arms; L1/L2/L3, segment 1, 2 and 3 of the labium; lbr, labrum; M, muscle with appropriate number (number of muscle corresponds to number in text, Figs. 9, 10, 12, 13 and Table 1); md, mandible; mx, maxilla; pcly, postclypeus; pis, piston of suspensorium; poc, postocciput; pta, posterior tentorial arm; ss, suspensorial sclerite.

apmp, apodeme of maxillary plate; ar, areolae; as, antennal socket; ata, anterior tentorial arm; atp, anterior tentorial pit; b, brain; ce, compound eye; cpc, circumesophageal connectives; ct, corpotentorium; ftg, first thoracic ganglion; g, gut; L1/L2, segment 1 and 2 of the labium; lbr, labrum; lor, lorum/mandibular plate; M, muscle with appropriate number (number of muscle corresponds to number in text, Figs. 9 and 11–13 and Table 1); md, mandible; mx, maxilla; nct, nucleus of connective tissue; oplo, optical lobe; pacl, paraclypeal lobe of Singh (1971); pcly, postclypeus; pd, pedicellus; poc, postocciput; pph, prepharynx; pta; posterior tentorial arm; ptp, posterior tentorial pit; sc, scapus; sd, common salivary duct of sd1 and sd2; sd2, salivary duct of accessory salivary gland; sp, sclerotised plate; sog, subesophageal ganglion; ss, suspensorial sclerite.

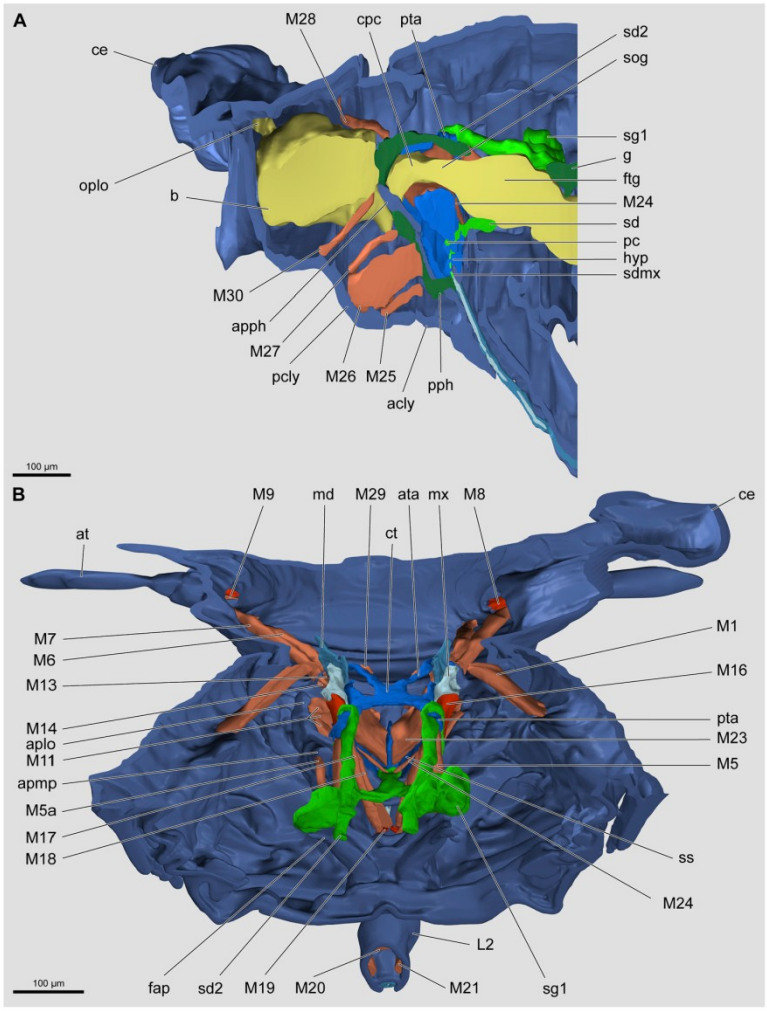

Fig. 12. *Hackeriella veitchi*, head and prothorax (legs omitted), 3D-reconstruction. A: sagital section, nervous and alimentary system with associated musculature. B: dorsal part of the specimen omitted (blue: sclerotization, light green: salivary system, dark green: alimentary system, red: musculature, yellow: nervous system). acly, anteclypeus; aplo, apodeme of lorum/mandibular plate; apmp, apodeme of maxillary plate; apph, apodeme attached to pharynx; ata, anterior tentorial arm; b, brain; ce, compound eye; cpc, circumesophageal connectives; ct, corpotentorium; fap, profurcal arms; ftg, first thoracic ganglion; g, gut; hyp, hypopharynx; L2, segment 2 of the labium; md, mandible; mx, maxilla; M, muscle with appropriate number (number of muscle corresponds to number in text, Figs. 9–11, 13 and Table 1); oplo, optical lobe; pc, pumping chamber; pcly, postclypeus; pph, prepharynx; pta, posterior tentorial arm; sd, common salivary duct of sd1 and sd2; sd2, salivary duct of accessory salivary gland; sdmx, salivary duct connecting pumpnig chamber with salivary channel of maxillae (indicated by the hypothetical green dotted line); sg1, principal salivary gland; sog, subesophageal ganglion; ss, suspensorial sclerite.

hypognathous condition. **M11** (loral apodeme-postclypeal muscle) of *Hackeriella* connects the postclypeus with the loral apodeme. In aphids, a presumably homologous muscle (m. laminae mandibularis primus + secundus) does not insert on the postclypeus, but on the anteclypeus. In *Hackeriella*, only one retractor muscle of the mandible (**M12** [M. craniomandibularis internus]) is present, whereas Singh (1971) described two retractors for *Hemiodoecus*. It is conceivable that Singh (1971) interpreted the slightly displaced anterior bundle as a second separate retractor muscle. In comparison with *Hackeriella* and considering the position of the tentorium, it appears unlikely that a second retractor "10" originates on the anterior tentorial arm, which would strongly limit its movability. In contrast to *Hackeriella*, the protractors of the mandible (**M13** [M. zygomaticus mandibulae] and **M14** [M. zygomaticus mandibulae]) originate on the lorum in *Hemiodoecus*, and not on the anterior tentorial arm as in *Hackeriella*. The third muscle (6) in this complex is not clearly distinguishable in *Hackeriella*. It is probably fused with M13 or (5), which are also inserted on the mesal side of the mandible. It is apparently due to the reduction of the tentorium in Heteroptera that the presumptive homologues of M13 and M14 are

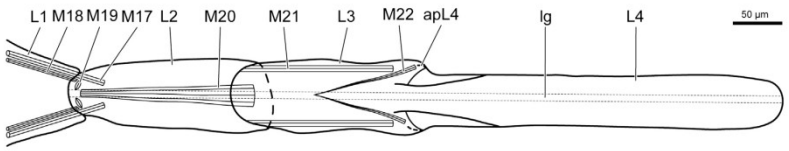

Fig. 13. *Hackeriella veitchi*, labium schematic (transparent), dorsal view. apl4, basal apodeme of segment 4 of labium; L, segment of labium with appropriate number; lg, labial groove; M, muscle with appropriate number (number of muscle corresponds to number in text, Figs. 10–12 and Table 1).

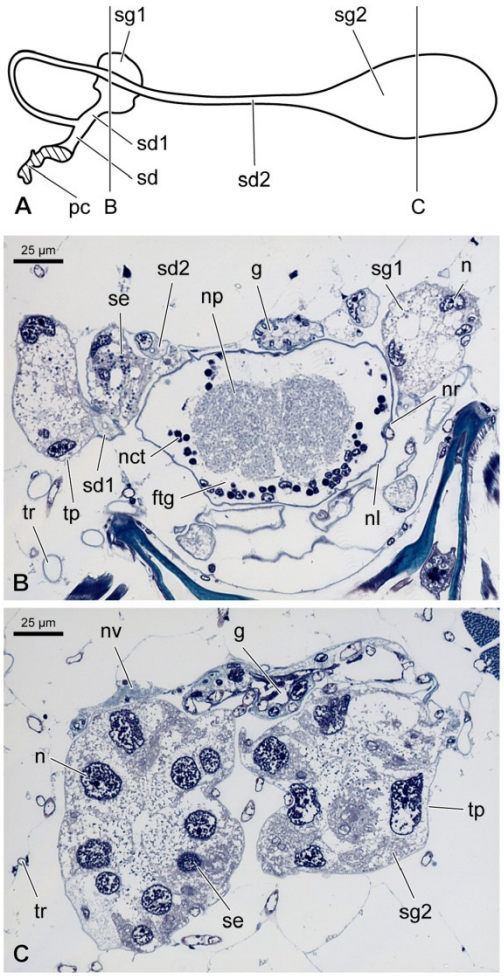

Fig. 14. *Hackeriella veitchi*, salivary gland complex and part of the nervous system. A: sagital section, schematic, cut surface hatched. The vertical lines indicate the plane of section in B and C. B: cross section of principal gland, plane of section in the prothorax. C: cross section of accessory gland, plane of section in the metathorax. ftg, first thoracic ganglion; g, gut; n, nucleus; nct, nucleus of connective tissue; nl, neural lamella; np, neuropilem; nr, neurilemma; nv, nerve; pc, pumping chamber; sd, common salivary duct of sd1 and sd2; sd1, salivary duct of principal salivary gland; sd2, salivary duct of accessory salivary gland; se, secretory granule; sg1, principal salivary gland; sg2, accessory salivary gland; tp, tunica propria; tr, trachea.

attached on other areas such as the clypeus or the lora in *Ochterus*, and not at the anterior tentorial arms. The second mandibular retractor KM9 (M. protractor setae mandibularis secundus) is only present in Ochteridae and Gelastocoridae, whereas Notonectidae and Aphelocheiridae are the only families of aquatic bugs lacking the first mandibular retractor KM10 (M. retractor setae mandibularis primus) (Rieger, 1976). The cardo, stipes and lacinia are not distinguishable in the maxilla of *Hackeriella*. Consequently, the homologisation of the maxillary protractor **M16** with the muscles listed by von Kéler (1963) (M. tentoriocardinalis or M. tentoristipitalis) and Wipfler et al. (2011) (M. tentoriocardinalis or M. tentoristipitalis anterior or M. tentoristipitalis posterior) is problematic. The same applies to the labial musculature. The glossa, paraglossa, and palps are reduced and cannot serve as a landmark for the labial retractor **M18**, which is likely equivalent with one of the two tentoriopremental retractors listed by von Kéler (1963). **M19** in the second labial segment is not mentioned by Singh (1971). However, in this case this is likely due to the simple dissection techniques, which are insufficient for the detection of very small muscles. This may also explain why no muscles corresponding with M24 and M28–M30 were identified by Singh (1971). A muscle occurring in aphids (m. add4, m. adductor quartus labii) is similar in position to M19 and likely homologous, even though it is extremely elongated compared to its counterparts in Heteroptera and Coleorrhyncha. **M20** is possibly homologous with M. submentomentalis of Wipfler et al. (2011). However, this remains uncertain due to the tube-like condition of the labium and the uncertain homology of its subunits. In contrast to the longitudinal muscle **M21** of the third labial segment in *Hackeriella*, muscle 26 of *Hemiodoecus* has a transverse orientation according to Singh (1971), as it is also the case with muscle 6 of *Saldula* and KM6 (M. transversalis labii tertius) of *Ochterus*. Muscle 23 of *Hemiodoecus* is associated with 24. The latter is not distinguishable as a separate bundle in *Hackeriella* and probably fused with the large longitudinal muscle M20 of the second labial segment. Particularly problematic is the interpretation of the labial muscles of *Corixa* as the homology of the labial subunits is unclear (see Benwitz, 1956; Rieger, 1976). Therefore, the homology of depr lb2 (m. depressor labii secundus) and **M22** remains uncertain as there is obviously no muscle in the third labial segment of *Corixa*. The partial reduction of the labium of *Corixa* probably resulted in the loss of muscles corresponding with M20 and M21. The homology assessment of **M24** and m. dil. cup1 (m. dilatator primus cupulae) of *Aphis* is also doubtful. Both muscles originate on the posterior region of the hypopharyngeal wings. However, the former does not insert on the salivary duct but instead on the pumping chamber. The homology of both muscles would imply a shift of insertion in *Hackeriella*. The absence of **M30** (M. frontobuccalis posterior) in *Aphis* is probably due to the fusion with the large cibarial dilator m. dil3 (m. dilatator tertius oris). In contrast to the aquatic bugs *Ochterus* and *Corixa*, **M30** is a single unit and not separated into two elements.

Muscle 59 (M. profurcacervicalis cruciatus) of von Kéler (1963) is defined by its origin on the profurca and its insertion on the cervical sclerites. Nevertheless, it appears likely that heteropteran

Table 1
Homologisation of musculature of *Hackeriella veitchi* with other representatives of Hemiptera, von Kéler (1963), Friedrich and Beutel (2008) and Wipfler et al. (2011). Unclear homologies set in parentheses, (/) not mentioned by the author, (–) muscle absent, (?) not mentioned by the author or further figures and descriptions for a clear conclusion are absent in the cited works.

Muscle of *Hackeriella veitchi*	Singh (1971) *Hemiodoecus leai*	*Systelloderes*	Rieger (1976) *Ochterus marginatus*	Benwitz (1956), Rieger (1976) *Corixa punctata*	Parsons (1962,1963) *Saldula pallipes*[c]	Weber (1928) *Aphis fabae*	Nomenclature of Wipfler et al. (2011)	Nomenclature of Friedrich and Beutel (2008)	Nomenclature of von Kéler (1963)
M1	–	M1	TM10b	rot cap1	T10	Odvm	/	Itpm1	61
M1a	–	M1a	TM1	ret cap1	T1	–	/	Idlm4	57
M2	47	M2	TM3	retr cap2	T3	Odlm	/	Idlm2	55
M3	(52)	(M3)	(TM2)	(depr cap)	(T2)	(Oism)	/	Idvm4	/
M4	45	–	–	–	–	m. tent2	0te2	/	/
M5	–	M5	TM6	retr cap3	T6	Ovlm4	/	Ivlm3	58
M5a	–	–	(KM24)	("feinfaseriger Öffnermuskel")	?	–	/	(Ivlm1)	(66)
M6	1	M6	KM21	depr sc	H21	ant1	0an1	/	1
M7	1	M7	KM20	lev ? sc	H20	ant4	0an2	/	2
M8	2	M8	KM23	M8[a]	H23	ant2	0an6	/	5
M9	2	M9	KM22	M9[a]	H22	ant3	0an7	/	6
M10	–	–	(TM11)	–	–	–	/	(Idvm5)	/
M11	–	–	–	–	–	m. lam. mand1 + 2	/	/	/
M12	7 + 10	M12	KM10	retr mand	H10	m. retr. mand1 + 2	0md1	/	11
M13	5 + 6	M13	KM8	protr mand	H8	m. protr. mand.	0md6	/	14
M14	4	M14	KM9	–	H9	–	0md6	/	14
M15	13	M15	KM13	retr max	H13	m. retr. max1 + 2	0mx1	/	15
M16	11	M16	KM12	protr max	H12	m. protr. max2 + 3	(0mx1/2) or (0mx3/4/5) or (0mx6/7)	/	(17 or 18)
M17	17	M17	KM2b	add lb1	H2	m. add1	0la5	/	29
M18	15	M18	KM2a	add lb2	H1.5	m. add2	(0la6)	/	(30)
M19	–	M19	KM3	depr lb1	H3	m. add4	/	/	/
M20	23 (+24)	M20	KM4	–	H4	m. add3	(0la10)	/	/
M21	26	M21	KM6	–	H6	m. trans5	/	/	/
M22	30	M22	KM7	(depr lb2)	H7	m. abd3	/	/	/
M23	41	M23	KM25	retr pist	H25	m. retr. pist2	0hy12	/	37
M24	–	–	–	–	–	(m. dil. cup1)	/	/	/
M25	31	M25	KM14	abd lbr	H14	m. dil1	0ci1	/	43
M26	33	M26	KM15	dil cib	–	m. dil2	0bu1	/	44
M27	34	M27	KM16	dil buc	H16	m. dil3	0bu2	/	45
M28	?	–	KM19	dil ph3 d	H19	–	0ph1	/	51
M29	?	–	KM18	dil ph3 v	H18	m. depr. phar.	0ph2	/	52
M30	–	M30	KM17 + KM17a	dil ph1 + dil ph2 + m. dilatator oris	H17	–	0bu3	/	46
–	–	M31	–	–	–	–	0md4	/	13
–	–	KM1	KM1	MuFa	H1	m. abd1 + 2	/	/	/
–	–	KM5	KM5	trans lb	H5	m. trans2 – 4	/	/	/
–	–	KM11	KM11	–	H11	–	0md3	/	12
–	–	RM	RM	con ph	?	RM[b]	0st1	/	68
–	–	TM7	TM7	lev cap	T7	Ovlm4	/	Ivlm3	59
–	–	TM10a	TM10a	rot cap2	–	–	/	(Idvm1/2/3)	63
–	–	–	–	–	–	m. tent1	0te2	/	/
–	–	–	–	–	–	m. protr. max1	(0mx3/4/5)	/	(17 or 18)
–	–	–	–	–	–	m. retr. pist1	/	/	/
–	–	–	–	–	–	m. dil. cup2	0hy8	/	39
–	–	–	–	–	–	m. dil. cup3	0hy7	/	38
–	–	–	–	–	–	m. dil. cup4	0hy7	/	38
–	–	–	–	–	–	m. dil.cup5	0hy7	/	38
–	–	–	–	–	–	m. trans1	/	/	/
–	–	–	–	–	–	m. add5	/	/	/
–	–	–	–	–	–	Ovlm1	/	Itpm2	/
–	–	–	–	–	–	Ovlm2	/	/	(64)
–	–	–	–	–	–	Ovlm3	/	/	(62)

[a] Muscles were not named in Benwitz (1956). Therefore, the nomenclature used for *H. veitchi* is applied.
[b] Forbes, 1977.
[c] "T" referring to number of musculature of thorax, "H" referring to number of musculature of head.

muscles with an insertion on the postocciptal processes are equivalent, as these processes are in a similar position as the cervical sclerites. M. dil. cup4 (m. dilatator quartus cupulae) (Weber, 1928) is very likely homologous to 38 (M. praementosalivarialis anterior) implying its presence in the groundplan of Hemiptera, in contrast to the statement of von Kéler (1963). The homology of Ovlm2 (m. ventralis labii secundus) (Weber, 1928) with muscle 64 (M. propleuracervicalis) (von Kéler, 1963) is uncertain. Both muscles originate on the propleura. However, the muscle in *Aphis* inserts on the maxillary plate whereas it is the region of the cervical sclerite in von Kéler (1963). Although Ovlm3 (m. ventralis labii tertius) (Weber, 1928) is not inserted on the ventral region of the posterior head capsule, it is apparently equivalent with the intersegmental muscle 62 (M. propleuropostoccipitalis inferior)

between the propleura and labial segment (von Kéler, 1963). M. proepisterno-postoccipitalis primus (TM 10a) and its equivalents in Heteroptera originate on the anterior region of the proepisternum and instert dorsally on the postoccipital apodeme, just like Idvm1 (M. cervico-occipitalis anterior), Idvm2 (M. cervico-occipitalis medialis) and Idvm3 (M. cervico-occipitalis posterior) of Friedrich and Beutel (2008). However, the latter originate on cervical sclerites which are absent in Heteroptera, which impedes the unambiguous homologisation of these muscles.

A muscle corresponding with **M31** is present in *Systelloderes* but not documented for any other heteropterans. It is a third mandibular retractor muscle (M. hypopharyngo-mandibularis) which originates at the posterior end of the hypopharyngeal wing and inserts ventrally on the widened part of the mandible. Additionally, few minute muscle fibres are present in the labium, which are apparently missing in other heteropterans.

In Coleorrhyncha and the groundplan of Heteroptera the maxilla is equipped with one protractor and one retractor. According to Rieger (1976) this is also the case in Sternorrhyncha and Auchenorrhyncha, implying that this configuration belongs to the hemipteran groundplan. However, as shown by Kramer (1950), this condition is only documented for Fulgoroidea, whereas there are two protractors and two retractors in Cicadidae and Cercopidae, and one protractor and two retractors in Cicadellidae. The two retractors of *Aphis* (m. primus setae maxillaris + m. secundus setae maxillaris, m. retr. max1 + 2) are likely two partitions of a single muscle. This also applies to both maxillary protractors (m. protractor secundus und tertius setae maxillaris, m. protr. max2 + 3), whereas m. protractor primus maxillaris (m. protr. max 1) is a separate muscle (Weber, 1928), which is in contrast to the generalizing statement of Rieger (1976). The mandible of heteropterans is moved by two protractors and two retractors in the groundplan according to Rieger (1976). Two protractors are also present in Coleorrhyncha, but only one retractor muscle. One retractor and one protractor are present in Sternorrhyncha according to Rieger (1976). However, in aphids there are two retractors (m. retractor primus setae mandibularis + m. retractor secundus setae mandibularis, m. retr. mand1 + m. retr. mand2), which we interpret as two partitions of a single muscle in agreement with Weber (1928). Both partitions have almost the same origin and insertion. In general, it is difficult to determine if there is a single retractor with distinct partitions or if there are multiple retractors each consisting of a single unit. The mandibles of Fulgoridae, Cicadidae, and Cercopidae are also operated with one retractor and one protractor. However, in Cicadellidae there are two retractors and even three in Membracidae (Kramer, 1950).

4.2. *The monophyly of Peloridiidae (Coleorrhyncha) and the supporting apomorphies*

Considering the very unusual features of Coleorrhyncha and the uniformity of the group, it is not surprising that its monophyly has never been questioned. Cephalic features are no exception: *Hackeriella*, *Pantinia* and *Peloridium* share a series of unusual and conspicuous features which are likely autapomorphies of Peloridiidae and Coleorrhyncha. The head is subtriangular and strongly compressed dorsoventrally, the globular compound eyes are widely separated, and oval areolae are present on the anterior head region. The loss of cephalic areolae in *Oiophysella* and *Craspedophysa* (Burckhardt, 2009) apparently took place two times independently within extant Peloridiidae. Another potential autapomorphy is the presence of two distinctive rows of sensilla at the apex of the labial rostrum (s. also Brozek, 2007: *X. cascus*). Another derived condition is the three-segmented antenna with a spindle-shaped flagellomere. Four antennomeres are present in the groundplan of Heteroptera (with some variation within the group) (e.g., Schlee, 1969; Zrzavý, 1990) and an aristate flagellum is possibly an autapomorphy of Auchenorrhyncha (e.g., Strümpel, 2010). Another potential autapomorphy of Coleorrhyncha is the partial coverage of the antennae by the genal area. This resembles the cryptic condition found in the heteropteran Nepomorpha ("Cryptocerata") (e.g. Benwitz, 1956; Rieger, 1976). This may be due to parallel evolution in these lineages. However, it is also conceivable that this is a derived groundplan feature of Heteropterodea, with reversal in the majority of the heteropteran subgroups (see Li et al., 2012).

The presence or absence of ocelli in Coleorrhyncha is likely linked with the presence or absence of the capacity of flight, a correlation also observed in other hemipterans (e.g., Schuh and Slater, 1995). Only *P. hammoniorum* has three lenticular ocelli (see Evans, 1981; Popov and Shcherbakov, 1991), the only species with developed hind wings and capable of flight (Burckhardt, 2009). This is apparently a groundplan feature of Hemiptera including Coleorrhyncha. The loss of all three ocelli could be interpreted as a potential synapomorphy of Peloridiidae excl. *Peloridium*, but this reduction is apparently linked with the complete loss of the hind wings. An additional apomorphic feature suggesting a basal position of *Peloridium* is the presence of a thin film covering nearly the entire surface of the body in all other genera (China, 1962). The basal placement would be in contrast to the phylogeny of Burckhardt (2009) where *Peloridium* is nested within Peloridiidae. This concept implies parallel losses of wings and ocelli and independent acquisitions of the surface film.

An apomorphic feature almost generally present in Coleorrhyncha is the absence of the ecdysial line (coronal and frontal sutures), which is usually a common landmark of the head capsule in Hemiptera (e.g. Hamilton, 1981) and other groups of insects. In the studied specimens of Coleorrhyncha it is not distinguishable. However, it was depicted in figures showing *Hemiodoecus* (Evans, 1937; Singh, 1971; Hamilton, 1981) and is therefore likely present in the groundplan of the group.

Other potential autapomorphies are character losses. A mandibular lever, mandibular glands, and a distinctly developed mandibular sac are missing. Based on Figs. 7 and 8 of Pendergrast (1962), Rieger (1976) assumed the presence of a mandibular lever without tendon in *X. cascus* and assigned a simple bar-shaped lever to the groundplan of Coleorrhyncha. A structure interpreted as a lever is documented for *Hemiodoecus* (Singh, 1971) but it is conceivable that this is a part of the plate-like basal mandibular region. The clearly documented absence in *Hackeriella*, suggests that the lever may be absent in the groundplan of Coleorrhyncha.

The maxillary sac is strongly reduced in *Hackeriella*. This and the greatly reduced ring muscle layer of the pharynx are additional potential autapomorphies of the suborder, but conformation for more species is required. A more or less continuous muscle layer of the pharynx (and the posterior parts of the foregut) is present in Heteroptera (e.g. Barth, 1952b; Benwitz, 1956; Rieger, 1976), and also in Sternorrhyncha (Forbes, 1977) and Auchenorrhyncha (Strümpel, 2010). Another potential autapomorphy is the absence of a cavity-like cibarial sense organ. The presence of this unusual structure in Heteroptera (e.g. Barth, 1952a, 1952b; Parsons, 1962; Parsons and Hewson, 1976; Swart and Felgenhauer, 2003), Auchenorrhyncha (Strümpel, 2010) and Sternorrhyncha (e.g., Forbes, 1977) suggests that this is a groundplan apomorphy of Hemiptera, with secondary loss in Coleorrhyncha.

Another unusual feature is the apparent absence of a recognizable separate frontal ganglion. However, this requires more detailed studies. Other unusual characteristics of the cephalic nervous system are the reduced condition of the neurilemma and

the presence of posteriorly directed tritocerebral processes connected by a loose meshwork of nerve fibres.

4.3. Synapomorphies of Coleorrhyncha and Heteroptera (Heteropterodea)

The sistergroup relationship between Coleorrhyncha and Heteroptera appears well supported. A potential synapomorphy is the distinctly reduced number of antennomeres with a total of four in the groundplan of Heteropterodea. The number is also reduced in the antenna of Auchenorrhyncha, which is composed of three segments (Strümpel, 2010), in some cases with a secondary subdivision of the flagellum (up to six subunits). However, the aristate type of antenna differs distinctly from what is found in Coleorrhyncha and Heteroptera. The number of antennomeres in Sternorrhyncha ranges from six or fewer (Aleyrodoidea, aphids, coccids) to 11 in Margarodidae (Grimaldi and Engel, 2005) or even 16 in some Coccina (Schmutterer, 2008). The presence of a distinct mandibular sulcus in Coleorryncha and the equivalent unit formed by the clypeal cleft and genal suture in Heteroptera (Parsons, 1962; Matsuda, 1965) is also a possible synapomorphy. Another shared feature is the absence of a clasping organ in the labial groove. Its presence in Auchenorrhyncha and Sternorrhyncha (Weber, 1930: "fingerförmige Fortsätze") is arguably a groundplan feature of Hemiptera, considering a possible basal position of the latter group (Cryan and Urban, 2012).

Another potential synapomorphy of Coleorrhyncha and Heteroptera is the absence of cervical sclerites (Benwitz, 1956). These structures are also missing in Sternorrhyncha (Singh, 1971), but this is likely due to parallel loss. In Auchenorrhyncha their presence is at least documented for the genus *Platypleura* (Cicadidae, Cicadomorpha) (Singh, 1971).

The long and slender accessory duct forms a loop within the head capsule in Coleorrhyncha and Heteroptera (Weber, 1930; Baptist, 1941). This is another potential synapomorphy of both groups.

A characteristic feature of the cephalic nervous system in Heteropterodea is the compact unit formed by the brain and the subesophageal ganglion, with greatly shortened circumesophageal connectives and a narrow passage for the pharynx (e.g. Graichen, 1936; Benwitz, 1956; Mahner, 1993). A very similar apomorphic condition has evolved independently in Antliophora (e.g., Beutel et al., 2011).

Muscular features shared by both groups are the presence of a small muscle between the head and thorax (M1a, M. pronotopostoccipitalis medialis), the presence of a second mandibular promotor (M14, M. zygomaticus mandibulae), the presence of a dorsal pharyngeal muscle M28 (M. verticopharyngalis) and M30 (M. frontobuccalis posterior).

4.4. Potential synapomorphies of Coleorrhyncha and "Homoptera"

As pointed out above, Coleorrhyncha were associated with Sternorrhyncha and Auchenorrhyncha by some authors (Myers and China, 1929; Evans, 1937, 1957, 1963; Singh, 1971). Characters potentially supporting "homopteran" affinities will be discussed in the following. According to Myers and China (1929) "the only universally valid character separating the two suborders, Heteroptera and Homoptera, is the presence or absence of a gula." Aside from the lacking gula, apparently a plesiomorphic feature, shared cephalic characters of Coleorrhyncha and "Homoptera" mentioned in this study are a labium which is not bent at its base and the separation of the antennal ledge from the frontal lobe (=paraclypeal lobe + lorum). The first two characters are unequivocally supported by the present study while the latter is one of doubtful value and at least not confirmed in *Systelloderes*. However, the absence of a gula is clearly a plesiomorphic feature.

Singh (1971) described the maxillary plates of Auchenorrhyncha as triangular plates each forming an internal distinct plate-like apodeme. This apodeme is developed in *Hackeriella*, but absent in various groups of Heteroptera, such as *Ochterus* (Ochteridae, Nepomorpha) (Rieger, 1976), *Corixa* (Corixidae, Nepomorpha) (Benwitz, 1956), Gerridae (Gerromorpha) (Matsuda, 1960), *Saldula* (Saldidae, Leptopodomorpha) (Parsons, 1962), *Triatoma* (Reduviidiidae, Cimicomorpha) (Barth, 1952a, 1952b) and *Systelloderes*. The second character listed by Singh (1971) is the presence of a complete or nearly complete tentorium, with reduced dorsal arms in Coleorrhyncha and Sternorrhyncha. Like the absence of the gula the well developed head endoskeleton is obviously a plesiomorphic condition.

The exclusive presence of the epistomal ridge in "Homoptera" (e.g. Spooner, 1938; Kramer, 1950; Singh, 1971) and Coleorrhyncha is also apparently a symplesiomorphic condition. The interpretation of the absence as a potential autapomorphy of Heteroptera (e.g. Spooner, 1938; Butt, 1943) is rejected. The epistomal ridge is present in the examined species of Enicocephalomorpha (Enicocephalidae) and, therefore, very likely in the groundplan of Heteroptera.

In a study on the maxillary plates, Bourgoin (1986a) considered the presence of the Evan's organ as a synapomorphy of Coleorrhyncha and Auchenorrhyncha, or alternatively as an autapomorphy of "Homoptera" (incl. Coleorrhyncha) with secondary reduction in Sternorrhyncha. This structure is present in *Hemiodoecus* according to Bourgoin (1986a), but is apparently missing in *Hackeriella* like in Heteroptera.

Another potential argument for homopteran affinities of Coleorrhyncha is the presence of M11 (loral apodeme-postclypeal muscle) in *Hackeriella* and of the similar muscles m. lam. mand1 (m. laminae mandibularis primus) and m. lam. mand2 (m. laminae mandibularis secundus) in *Aphis* (Aphididae, Sternorrhyncha) (Weber, 1928). Whether this muscle is present or absent in Auchenorrhyncha is presently unclear.

A reliable interpretation of the features listed here requires a formal analysis of a broad set of characters. However, based on the results of older (e.g., Schlee, 1969) and more recent studies (e.g., Bourgoin and Campbell, 2002; Cryan and Urban, 2012) based on morphological or molecular data it appears likely that features shared by Coleorrhyncha and "homopteran" lineages are either plesiomorphic or due to parallel evolution.

4.5. Autapomorphies of Heteroptera and features indicating relationships within the suborder

A potential autapomorphy of Heteroptera is the loss of the median ocellus (Jordan, 1972; Schuh and Slater, 1995). Three ocelli belong to the groundplan of Coleorrhyncha, Auchenorrhyncha and Sternorrhyncha, even though losses occur in all three lineages (e.g., Weber, 1928; Breider, 1952; Bährmann, 2002; Strümpel, 2010). Within Heteroptera, groups without paired ocelli occur in each of the infraorders (e.g., Mahner, 1993; Hebsgaard et al., 2004; Schuh et al., 2009). This clearly suggests multiple losses.

The presence of a gula is another potential autapomorphy of Heteroptera (e.g., Parsons, 1962; Rieger, 1976; Schuh and Slater, 1995). This is in contrast to a statement in Hamilton (1981) and Grimaldi and Engel (2005), who considered the gula as a synapomorphy of Coleorrhyncha and Heteroptera, and Carver and Gross (1991), who included Coleorrhyncha in Heteroptera based on the alleged presence of this structure. This structure is always absent in Coleorrhyncha (Myers and China, 1929; Schlee, 1969; Evans, 1981; Burckhardt, 2009; Larivière et al., 2011) and this is also the case in

Auchenorrhyncha and Sternorrhyncha (Spooner, 1938). A correlated plesiomorphic condition found in these three lineages is the hypognathous head. However, this character state is also maintained in several groups of Heteroptera, despite of the presence of a gula (e.g., Weber, 1929; Rieger, 1976). A prognathous head is a characteristic feature of several predaceous lineages of Heteroptera, such as for instance Enicocephalomorpha, Gerromorpha, and Reduviidae (e.g. Barth, 1953a; Wygodzinsky and Schmidt, 1991; Schuh and Slater, 1995). It is presently unclear whether this is a derived groundplan feature of the suborder with reversal in several groups, or whether prognathism has evolved several times independently.

Another autapomorphy of Heteroptera is the strongly reduced tentorium (Rieger, 1976: *Ochterus* [Ochteridae, Nepomorpha]; Cranston and Sprague, 1961: *Gerris* [Gerridae, Gerromorpha]; *Systelloderes*), in contrast to the largely complete cephalic endoskeleton of Coleorrhyncha, and correlated shifts of muscles (see above). Bourgoin (1986b) documented a slender apodeme connected to the mandibular lever for some members of Nepomorpha (*Notonecta* sp., Notonectidae) and Pentatomomorpha (Pentatomidae). He suggested the homology of this structure with the anterior tentorial arm of Fulgoromorpha. However, the putative homologue in *Hackeriella* is not inserted internally on a mandibular lever (which is in fact absent) but directly on the head capsule. This impedes an unambiguous interpretation and apparently this issue requires further investigation. Anterior tentorial arms ("cranial apodemes of the antennal musculature" of Rieger, 1976) are absent in Gerridae (Matsuda, 1960) and Ochteridae (Rieger, 1976). The homology assessment of the "dorsal apodeme" of *Saldula* (Saldidae, Leptopodomorpha) (Parsons, 1962) and the anterior tentorial arm of *Hackeriella* is problematic. Both structures are areas of origin of antennal muscles. In *Saldula* the mandibular retractor also originates from the apodeme, whereas the protractor arises from the anterior arm in *Hackeriella*. Therefore, the homology of the "distinct indentation" (see Fig. 1 of Parsons, 1962) and the anterior tentorial pit is also uncertain. Barth (1952a, 1952b) described a tentorium for Triatominae (Reduviidae, Cimicomorpha). The absence of an appropriate reconstruction impedes the interpretation of some elements, but it is conceivable that they are parts of the hypopharyngeal wings, the maxillary lever, or the mandibular or maxillary sac. In *Systelloderes* no traces of a tentorium are present. The condition in the potentially basal heteropteran lineage Dipsocoromorpha is still unknown (Weirauch and Schuh, 2011). Different degrees of reduction occur in Auchenorrhyncha and Sternorrhyncha, but a well developed tentorium is at least present in the groundplan of the former group (e.g. Cercopidae (Cicadomorpha); Spooner, 1938; Singh, 1971; Strümpel, 2010).

Another apomorphic feature occurring in most groups of Heteroptera is the loss of the epistomal ridge (transverse frontoclypeal strenghtening ridge, "fronto-clypeal suture") (Spooner, 1938; Butt, 1943). However, the ridge is present in Enicocephalomorpha (see above) and therefore very likely in the groundplan of the group. In *Belostoma* (Belostomatidae, Nepomorpha) (Verma et al., 1973) the frons is separated from the clypeus by a "postclypeus groove", and in *Nepa* (Nepidae, Nepomorpha) by a tenuous "frontal suture" (Hamilton, 1931), structures likely representing a modified or partly reduced epistomal ridge. The epistomal ridge is not only well developed in Coleorrhyncha, but also in most groups of Auchenorrhyncha (absent in some Cercopidae, Jassidae Membracidae; distinct in Cicadidae, Fulgoridae and Flatidae) (e.g. Spooner, 1938; Kramer, 1950; Singh, 1971) and at least in some representatives of Sternorrhyncha (Margarodidae [Coccoidea], Aphididae [Aphidoidea], Psyllidae [Psylloidea]; Singh, 1971). A derived feature described for members of different lineages of Heteroptera is the presence of two or four distinct lateral postoccipital spurs (Spooner, 1938; "condylus" of *Triatoma* [Reduviidae, Cimicomorpha] (Barth, 1952a, 1952b); "Kehlsporn" of *Corixa* [Corixidae, Nepomorpha] (Benwitz, 1956); "long apodemes" of *Gerris* [Gerridae, Gerromorpha] (Cranston and Sprague, 1961); "occipital condyles" in *Saldula* [Saldidae, Leptopodomorpha] (Gupta, 1961; Parsons, 1962); "ventrales Apodem" and "dorsales Apodem" of *Ochterus* [Ochteridae, Nepomorpha] (Rieger, 1976)). The elements of the "posterior tentorium" illustrated by Hamilton (1981) for Nepomorpha ("Cryptocerata") are apparently homologous to these structures. We consider the presence of the spurs as another potential autapomorphy of Heteroptera. The postoccipital margin is smooth in Coleorrhyncha, and this is also the case in Sternorrhyncha (Singh, 1971) and most groups of Auchenorrhyncha. Two "occipital condyles" occurring in cicadellid and membracid species examined by Kramer (1950) have very likely evolved independently.

Another apomorphic feature characterizing Heteroptera is a narrowed occipital foramen, which is only adjacent with a part of the postoccipital region (e.g. Benwitz, 1956; Hamilton, 1981). A correlated feature is the anterior shift of the labium. The corresponding plesiomorphic conditions are preserved in Coleorrhyncha and Auchenorrhyncha, where the foramen is very large. Extensive parts of the postoccipital region are involved in its formation and the labium is attached close to its ventral margin (e.g., Kramer, 1950; Singh, 1971).

The ventral anterior regions of the maxillary plates of Heteroptera are transformed into bucculae and partly enclose the base of the labium (e.g. Barth, 1953b; Kumari, 1955). These projections are an additional guiding and protection for the labium. This is arguably another groundplan apomorphy of Heteroptera. However, in some members of the group they are rudimentary or completely absent, as it is also the case in Coleorrhyncha (Spooner, 1938).

Intersegmental sclerites located between antennomeres three to four ("intraflagelloid") are another potential autapomorphy of Heteroptera (Zrzavý, 1990, 1992). However, Mahner (1993) rejected the presence of an "intraflagelloid" in the groundplan of the group, and interpreted this feature as an apomorphy of Heteroptera excluding Nepomorpha. The presence of similar sclerites between segments two to three ("preflagelloid") was considered as a potential synapomorphy of Heteroptera and Coleorrhyncha by Zrzavý (1990, 1992). As our own histological sections show that a "preflagelloid" is absent in Peloridiidae, this is another possible autapomorphy of Heteroptera.

Mandibular levers are probably present in the groundplan of Hemiptera (see below). However, the presence of three different forms (Rieger, 1976) is a potential apomorphy of Heteroptera.

Another potential autapomorphy is the presence of two intercalary sclerites situated in the dorsal region of the membrane between the labial segments three and four. This feature is recorded for some aquatic heteropterans (Mahner, 1993), and similar structures are also documented for few members of Cimicomorpha (Reduviidae, Pachynomidae, Plokiophilidae) (Cobben, 1978). Whether this feature belongs to the groundplan of the suborder is unclear presently.

The maxillary stylets of some groups of Heteroptera are equipped with rows of hairs functioning as a filter (e.g. Belostomatidae [Nepomorpha] (Kopelke, 1978), Ochteridae [Nepomorpha] (Rieger, 1976) and Saldidae [Leptopodomorpha] (Parsons, 1962)). A reliable phylogenetic interpretation is presently not possible. These structures are absent in Pentatomomorpha like in Coleorrhyncha, Sternorrhyncha (Cobben, 1978) and Auchenorrhyncha (Strümpel, 2010).

An unusual feature occurring in heteropteran lineages is the interlocking mechanism of the edges of the labial groove, which is present in Enicocephalomorpha, Gerromorpha, and in Reduviidae (Cimicomorpha) ("Mandibelklammer") (Barth, 1953a; Cranston and

Sprague, 1961). The phylogenetic significance of this specialised condition is also unclear.

The food pumps of a few members of predaceous heteropterans are equipped with sclerotised nodes and ridges at their epipharyngeal and hypopharyngeal regions ("triturating devices") (Nepomorpha (Swart and Felgenhauer, 2003); *Saldula*, Leptopodomorpha (Parsons, 1962)). These structures are used for crushing and grinding particles in the food stream (e.g. Parsons, 1972; Parsons and Hewson, 1976).

The principal salivary gland is usually bilobed in Heteroptera (Southwood, 1955; Miyamoto, 1967; Mahner, 1993) and its duct is strongly reduced and shortened. These are also potential heteropteran autapomorphies. The presumably basal Enicocephalomorpha, Dipsocoromorpha, Gerromorpha and Nepomorpha differ from the remaining groups by an aciniform principal salivary gland with few large cells with a narrow lumen and a smooth surface (Miyamoto, 1967; Cobben, 1978). It is conceivable that this is an apomorphic groundplan feature of Heteroptera, with secondary modifications in different lineages.

4.6. Potential autapomorhies of Hemiptera

Like in other groups of Hemiptera (Spooner, 1938) the clypeus of Coleorrhyncha is subdivided into an anteclypeus, a postclypeus, and a paraclypeus. This is possibly a derived groundplan feature of this large lineage, but this needs further confirmation. Another complex of hemipteran autapomorphies is linked with the labrum (e.g. Spooner, 1938; Parsons, 1962; Hamilton, 1981), i.e. the reduction in size, the specific function as the dorsal closure of the base of the feeding tube, the absence of muscles (e.g., Weber, 1928; Parsons, 1962; Rieger, 1976), and the related immobilization.

The transformation of the mandibles into stylets is also a potential autapomorphy. However, it was already pointed out by Hennig (1969) that this is also a potential synapomorphy with Thysanoptera, like the greatly modified maxillae, which are stylet-like (laciniae), linked with each other to form a food canal, and completely lack a galea and palp (e.g. Forbes, 1969; Schuh and Slater, 1995; Brozek and Herczek, 2001; Swart and Felgenhauer, 2003; Brozek and Herczek, 2004; Brozek et al., 2006). The detachment of the lacinia from the stipes is considered as a groundplan feature of the entire Acercaria (see e.g., Grimaldi and Engel, 2005). This condition was not found in *Hackeriella*, apparently a result of reversal. The linkage of the maxillae could not be documented in this study. In all examined specimens of Peloridiidae they were widely separated from each other at the thickest point near their bases. It is likely that all members of the family can link their maxillae to form a food and salivary channel as it was documented for *P. hammoniorum* by Cobben (1978) and *X. cascus* by Brozek (2007). The food canal of Hemiptera is formed to equal degrees by both stylets. In contrast, the salivary canal is mainly formed by a longitudinal concavity on the right maxilla in Heteropterodea and Auchenorrhyncha (Fulgoroidea), but by a similar furrow on the left maxilla in Sternorrhyncha (Coccinea) (e.g. Cobben, 1978; Brozek, 2006, 2007; Brozek et al., 2006). A reduction of the salivary channel occurs in predaceous groups of Heteroptera (e.g. Barth, 1952b; Matsuda, 1965). An unusual condition is the presence of only one canal for both saliva and food in *Hydrometra* (Hydrometridae, Gerromorpha) (Sprague, 1956; Cobben, 1978).

Rieger (1976) assigned the presence of mandibular levers to the groundplan of Hemiptera. He defined this structure as a sclerotised plate connecting the head capsule with the mandibular stylet with or without a tendon. Three groups of mandibular levers are generally present in Heteroptera according to Rieger (1976), whereas the mandibular levers are simple bar-shaped sclerites in Auchenorrhyncha and Sternorrhyncha (partim). The absence in Psyllina and the Y-shape in Aleurodina are potential autapomorphies of these lineages, respectively (Rieger, 1976). Whether a lever is present or absent in the groundplan of Coleorrhyncha is presently unclear (see above).

Barb-like structures at the tip of the mandibular stylets for anchoring in the host tissue are generally present in the hemipteran subgroups (e.g. Forbes, 1977; Schuh and Slater, 1995; Swart and Felgenhauer, 2003; Strümpel, 2010). This derived condition is likely an additional autapomorphy of the lineage.

A sclerotised bar-shaped maxillary lever is probably present in the groundplan of Hemiptera and Heteroptera (Rieger, 1976). In the latter group (e.g., Ochteridae, Potamocoridae, Gelastocoridae, Leptopodomorpha, Pentatomomorpha, Pachynomidae; see Parsons, 1962; Cobben, 1978; but also in *Systelloderes*) it is apparently more important as a guiding device for the maxillary stylets than as a muscle attachment site (Rieger, 1976). The absence in many heteropteran groups (Notonectidae, Pleidae, Aphelocheiridae, Nepidae, Belostomatidae, Corixidae, Gerridae, *Hydrometra*, Aradidae, Reduviidae, *Cimex*; see Matsuda, 1960, 1965; Rieger, 1976; Cobben, 1978) is likely due to parallel reduction. In Coleorrhyncha, where it is also absent, the suspensorial sclerites, the maxillary plates and the mandibles function as a guiding device of the maxillary stylets. The lever is generally present in Auchenorrhyncha and Sternorrhyncha and serves as an insertion site for muscles (Matsuda, 1965).

Another complex apomorphic feature shared by Coleorrhyncha and the three other hemipteran lineages is the presence of a characteristic labial sheeth (rostrum) for the stylet-like paired mouthparts, and the complete lack of palps and typical endite lobes (e.g., Spooner, 1938; Singh, 1971; Burckhardt, 2009). In contrast to Coleorrhyncha, the number of labial subunits varies from three to four in Heteroptera (e.g. Hamilton, 1931; Jordan, 1972; Schuh and Slater, 1995; Weirauch, 2008), with the three-segmented condition probably resulting from the reduction of the basal element (Schuh and Slater, 1995). The number of labial segments in the groundplan of Auchenorrhyncha is disputed. Four are ancestral according to Singh (1971), but only three according to Butt (1943), Matsuda (1965), Kramer (1950) and Strümpel (2010) documented three for Cicadidae and four for Fulgoridae and other groups. In Sternorrhyncha five segments occur in some aphids (Lachnini) (Spooner, 1938), and four to none in some (female) Coccina (Matsuda, 1965; Schmutterer, 2008).

The morphology of the salivary pump is relatively uniform across Hemiptera and its presence and configuration is a complex autapomorphy. In the groundplan it is composed of a pumping chamber, a piston (reduced to a thin membrane in Psyllidae and Aleurodidae), a thickened membrane connecting these elements, and one (Coleorrhyncha, Heteroptera, Auchenorrhyncha) or two muscles (Sternorrhyncha) moving the piston (e.g Weber, 1930; Matsuda, 1965).

In the groundplan of Hemiptera each of the paired principal salivary glands ("main glands" of Hamilton, 1931; "Prothorakaldrüsen" of Benwitz, 1956) are connected with an accessory salivary gland ("subsidiary glands" of Hamilton, 1931) (Baptist, 1941; Cobben, 1978). This is likely an additional autapomorphy. Different modifications occur in the subgroups (see above).

Little information exists on the mandibular glands of specific members of Hemiptera. Linder (1956) described the secretion products for *Oncopeltus fasciatus* (Lygaeidae, Pentatomomorpha) but not the morphology. In *Schizaphis* (Aphididae, Sternorrhyncha) the common duct of the principal and accessory glands entering the salivary channel of the maxillae is complemented by a common duct of the maxillary and mandibular glands (Saxena and Chada, 1971). The mandibular glands are elbow-shaped and close to the maxillary gland and the subesophageal ganglion (Saxena and Chada, 1971).

Maxillary glands are commonly found in Hemiptera (Qadri, 1949) and also occur in Protura, Collembola, Neuroptera, Trichoptera, Hymenoptera and coleopteran larvae (Snodgrass, 1935; Linder, 1956). Tubular or aciniform maxillary glands ("cephalic glands") are at least present in the aquatic heteropteran lineages and in some members of Pentatomomorpha (*Pyrrhocoris, Dysdercus* [Pyrrhocoridae]; *Oncopeltus fasciatus* [Lygaeidae]) and Cimicomorpha (*Miris* [Miridae]) (e.g. Hamilton, 1931; Benwitz, 1956; Linder, 1956). They are apparently absent in *Systelloderes* and definetely missing in Coleorrhyncha. In Auchenorrhyncha they are only documented for Cicadellidae (Qadri, 1949). The description of Evans' organ in Fulgoromorpha (Bourgoin, 1986a) suggests that this structure may be homologous to the maxillary gland, but this interpretation remains uncertain. Both structures are associated with the maxilla or maxillary plate and a glandular function is also likely in the case of Evans' organ. However, ontogenetic and embryological studies are necessary to confirm this interpretation.

Presently there are two competing hypotheses on the evolutionary orgin and homology of the maxilla-maxillary plate-complex. The appendicular concept of Evans (1973) suggests that (1) the maxillary plate is homologous to the stipes (or the fusion of stipes and galea) of a generalized insect; (2) the maxillary plate is limited dorsad by the maxillary suture which is homologous to the subgenal ridge; (3) the Evans' organ is homologous to a modified maxillary palp. In contrast, in the parietal concept of Parsons (1964, 1974) the maxillary plate is described as a derivative of the genal-postgenal region. A review of both theories was presented by Bourgoin (1986a), who supported the parietal concept and rejected the homology of the maxillary suture with the subgenal ridge and the homology of Evans' organ with the maxillary palp. An unambiguous clarification of points (2) and (3) of Evans (1937) is presently not possibley as embryological data are lacking. In *Hackeriella* muscles without equivalents in more generalized insects are connected with the maxillary plate (M3, pronotal muscle of the maxillary plate; M5a, M. profurcacervicalis). The maxillary protractor M16 and its equivalents in Heteroptera (including *Systelloderes*) and *Aphis* originate on the maxillary plate and insert on the basal part of the maxillary stylet. The homology of the plate with the stipes (1) (Evans, 1973) would imply that these muscles are homologous to the intrinsic maxillary muscles 0mx6 (M. stipitolacinialis) or 0mx7 (M. stipitogalealis) of generalized insects (Wipfler et al., 2011). In contrast, the genal origin of the maxillary plate would imply that the maxillary protractor M16 is homologous to 0mx1 (M. craniocardinalis) or 0mx2 (M. craniolacinialis), which originate on the head capsule. Apparently, the configuration of muscles is not sufficient for the clarification of the origin of the maxillary plate. As pointed out above additional embryological studies are required.

5. Conclusions

The cephalic features investigated support the monophyly of Coleorrhyncha, Heteroptera, Heteropterodea, and of Hemiptera. Coleorrhyncha display an intriguing mixture of plesiomorphic (e.g., lack of a gula, almost complete tentorium) and highly derived features (e.g., strongly flattened subtriangular head with areolae, reduced pharyngeal muscularis). Synapomorphies of Coleorrhyncha and Heteroptera are the presence of a distinct mandibular sulcus, the reduced number of antennomeres, a labium without a clasping organ in the labial groove, coiled accessory salivary ducts, a compact unit formed by the brain and subesophageal gangion, the presence of a small cervical muscle M1a (M. pronotopostoccipitalis medialis), a second mandibular promotor (M14), a dorsal pharyngeal muscle M28 (M. verticopharyngalis), and a precerebral dilator M30 (M. frontobuccalis posterior). Shared derived features of Coleorrhyncha and homopteran groups are apparently either plesiomorphic or due to homoplasy. The monophyly of Heteroptera and Hemiptera are also well supported by cephalic features. Heteropteran autapomorphies include the gula and the strongly reduced condition of the tentorium with correlated muscle shifts. The transformation of the labium into a specific rostrum and a complex salivary pump are two of many convincing autapomorphies of Hemiptera.

The phylogenetic interpretations presented here are preliminary. They require confirmation by a formal character analysis, which will be conducted in a future study, when more detailed and well documented data for different hemipteran groups are available.

The head structures of Coleorrhyncha and Heteroptera are quite similar with respect to important functions, especially the food uptake. They do not provide easy explanations why the former suborder is a very small relict group and the latter extremely successful. A very unusual feature of the moss-feeding Coleorrhyncha is the extremely reduced condition of the pharyngeal ring muscle layer. It is conceivable that a secondary shift of diet, as it frequently occurs in Heteroptera, was not possible any more in Coleorrhyncha. This lacking ability to make use of a broad variety of food resources may have been one factor preventing a successful radiation as it took place in Heteroptera. A non-cephalic feature which is likely related with the low diversity is the strong tendency to reduce the flight organs. This applies also to other non-related orders with a very low diversity such as Zoraptera, Mantophasmatodea and Grylloblattodea, which like Coleorrhyncha comprise less than 40 described extant species.

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Corrections to Spangenberg et al. (2013a)

The extended taxon sampling of the present study, i.a. *Philaenus spumarius* (Auchenorrhyncha]) suggests that the apodeme “aplo” of *Hackeriella* and the corresponding muscle M11 is likely a remnant of the mandibular lever which is partly fused with the head capsule on its base. With respect to these new insights one consider the three partitions of M11 in Spangenberg et al. (2013a) as homologous to the mandibular protractors M13 and M14 (and should renamed like that) and to muscle 6 of *Hemiodoecus* in Singh (1971). M13 and M14 in *Hackeriella* (Spangenberg et al. 2013a) are two partitions of a single retractor muscle and homologous to M12c in Spangenberg et al. (2013b) (= muscle 10 of Singh (1971). This interpretation differs strongly from that presented in Spangenberg et al. (2013a). Consequently, a corrected data matrix and figures (see below) are presented in this study.

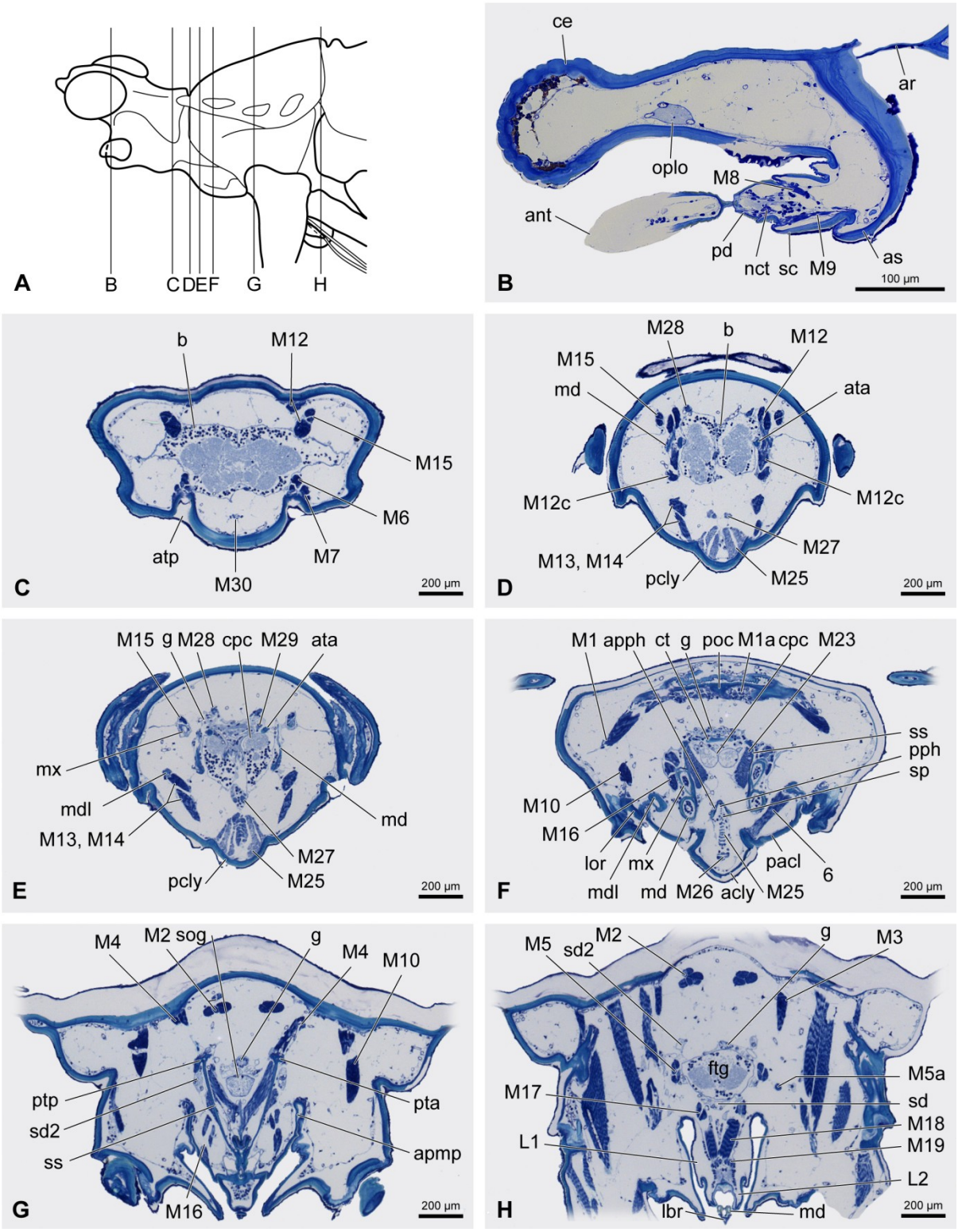

Fig. 10 (corrected). *Hackeriella veitchi*, cross sections. A: head and thorax, schematic, lateral view showing planes of section of light micrographs B–H. B: only left part of head is shown, apical part of antennomere and connection to areolae damaged; G: for detailed lettering see Fig. 9A–B. acly, anteclypeus; ant, antennomere; apmp, apodeme of maxillary plate; ar, areolae; as, antennal socket; ata, anterior tentorial arm; atp, anterior tentorial pit; b, brain; ce, compound eye; cpc, circumesophageal connectives; ct, corpotentorium; ftg, first thoracic ganglion; g, gut; L1/L2, segment 1 and 2 of the labium; lbr, labrum; lor, lorum/mandibular plate; M, muscle with appropriate number; md, mandible; mdl, mandibular lever; mx, maxilla; nct, nucleus of connective tissue; oplo, optical lobe; pacl, paraclypeal lobe of Singh (1971); pcly, postclypeus; pd, pedicellus; poc, postocciput; pph, prepharynx; pta; posterior tentorial arm; ptp, posterior tentorial pit; sc, scapus; sd, common salivary

duct of sd1 and sd2; sd2, salivary duct of accessory salivary gland; sp, sclerotized plate; sog, subesophageal ganglion; ss, suspensorial sclerite.

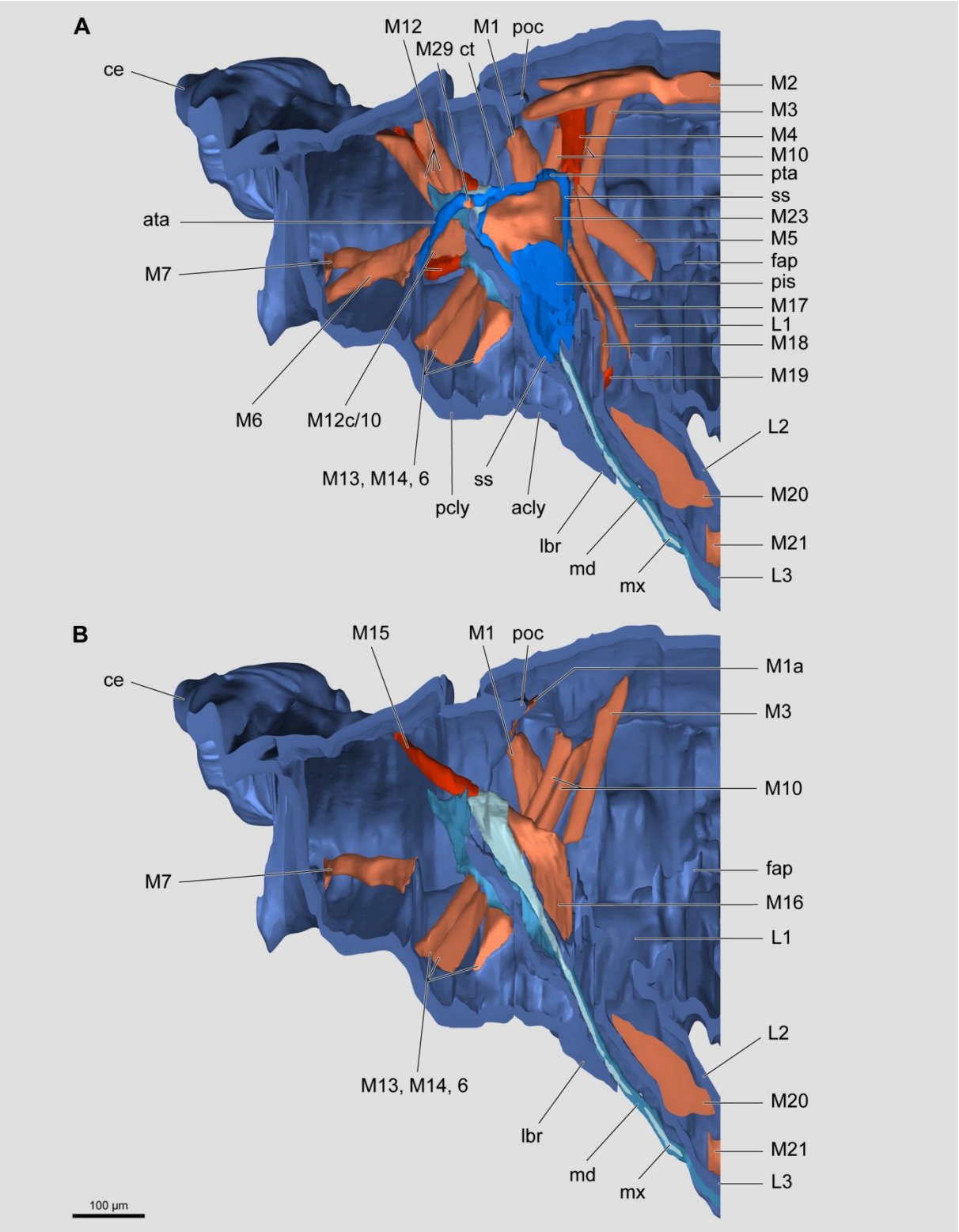

Fig. 11 (corrected). *Hackeriella veitchi*, head and prothorax (legs omitted), 3D-reconstruction, sagittal section, different muscles shown, tentorium omitted in B (blue: sclerotization, red: musculature). Areolae and forehead slightly rammed during fixation. acly, anteclypeus; ata, anterior tentorial arm; ce, compound eye; ct, corpotentorium; fap, profurcal arms; L1/L2/L3, segment 1, 2 and 3 of the labium; lbr, labrum; M, muscle with appropriate; md, mandible; mx, maxilla; pcly, postclypeus; pis, piston of suspensorium; poc, postocciput; pta, posterior tentorial arm; ss, suspensorial sclerite.

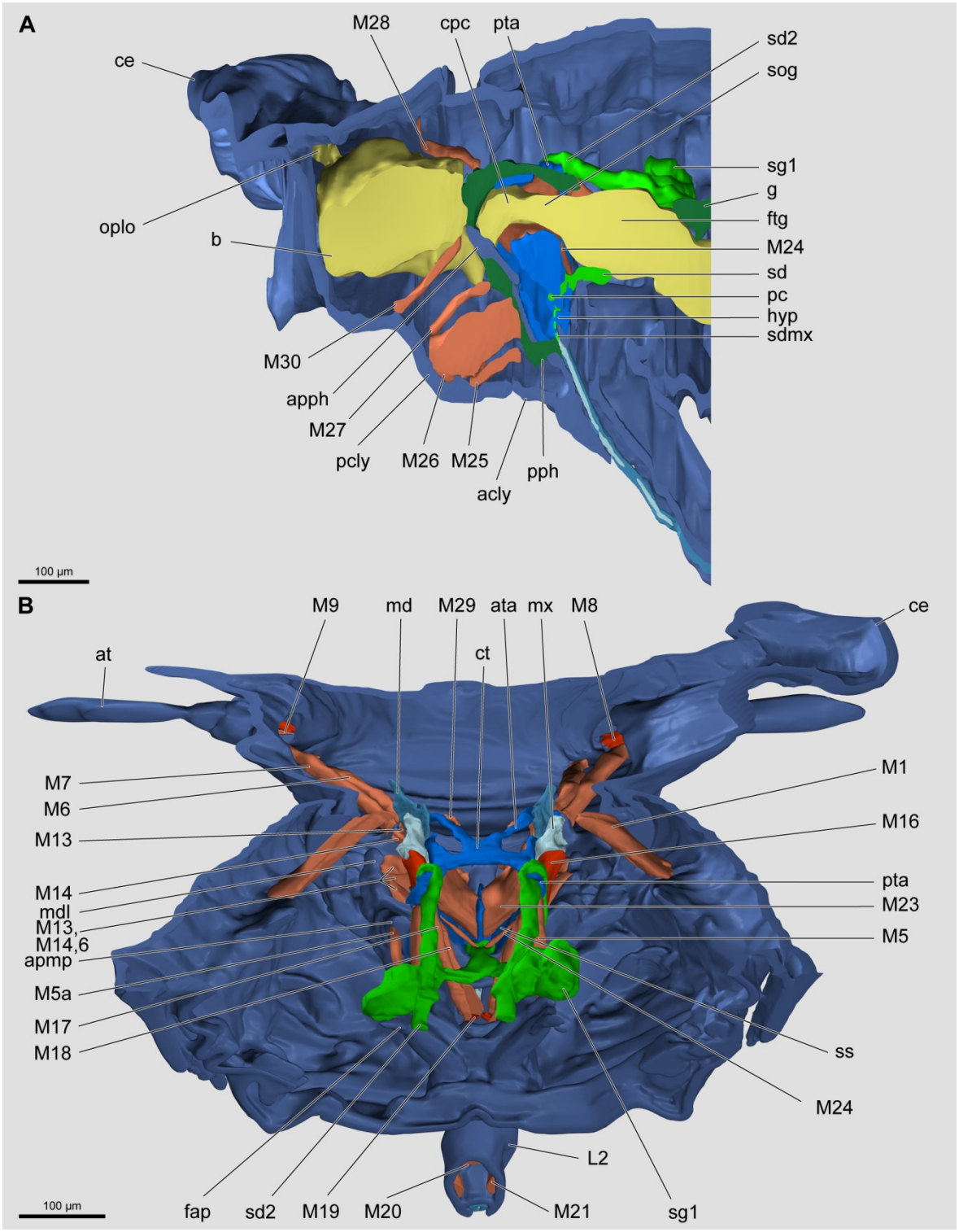

Fig. 12 (corrected). *Hackeriella veitchi*, head and prothorax (legs omitted), 3D-reconstruction. A: sagital section, nervous and alimentary system with associated musculature. B: dorsal part of the specimen omitted (blue: sclerotization, light green: salivary system, dark green: alimentary system, red: musculature, yellow: nervous system). acly, anteclypeus; apmp, apodeme of maxillary plate; apph, apodeme attached to pharynx; ata, anterior tentorial arm; b, brain; ce, compound eye; cpc, circumesophageal connectives; ct, corpotentorium; fap, profurcal arms; ftg, first thoracic ganglion; g, gut; hyp, hypopharynx; L2, segment 2 of the labium; md, mandible; mdl, mandibular lever; mx, maxilla; M, muscle with appropriate number; oplo, optical lobe; pc, pumping chamber; pcly, postclypeus; pph, prepharynx; pta, posterior tentorial arm; sd, common salivary duct of sd1 and sd2; sd2, salivary duct of accessory salivary gland; sdmx, salivary duct connecting pumpnig chamber with salivary channel of maxillae (indicated by the hypothetical green dotted line); sg1, principal salivary gland; sog, subesophageal ganglion; ss, suspensorial sclerite.

3.1.3 Study II

Friedemann K, **Spangenberg R**, Yoshizawa K, Beutel RG (2013). Evolution of attachment structures in the highly diverse Acercaria (Hexapoda). Cladistics 2013, 1–32.

Abstract: Acercaria display an unusually broad array of adhesive devices occurring on different parts of the legs. Attachment structures of all major subgroups are described and illustrated. Nineteen characters of the distal leg region were combined with a data matrix containing 99 additional morphological characters of different body parts. The results of the cladistic analysis are largely congruent with current hypotheses. Zoraptera are not retrieved as close relatives of Acercaria. The monophyly of the entire lineage and of the major subgroups Psocodea, Phthiraptera, and Hemiptera is confirmed. Our data also support the monophyly of Auchenorrhycha and a sister-group relationship between Thysanoptera and Hemiptera (Condylognatha). In contrast to other lineages of insects, the hairy type of adhesive device is present only in one group within the Acercaria (Heteroptera, Cimicomorpha). The arolium is present in the ground plan but missing in several groups (e.g. Psocodea, Cicadoidea, Aphidoidea). Pretarsal pulvilli evolved several times independently. Tarsal euplantulae and different specialized clasping devices have evolved within Phthiraptera, whereas pretarsal attachment devices are missing in this ectoparasitic group. The potential to modify pretarsal attachment devices in their structural details has probably contributed to the very successful diversification of the predominantly phytophagous Hemiptera.

Significance in the present thesis: This study compiles a traditional morphological data set (head, thorax, abdomen) and adds valuable information concerning tarsal and pretarsal attachment structures. Key-taxa such as Coleorrhyncha and Troctomorpha were part of the cladistic analysis.

Own contribution: 10%

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Evolution of attachment structures in the highly diverse Acercaria (Hexapoda)

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Abstract

Acercaria display an unusually broad array of adhesive devices occurring on different parts of the legs. Attachment structures of all major subgroups are described and illustrated. Nineteen characters of the distal leg region were combined with a data matrix containing 99 additional morphological characters of different body parts. The results of the cladistic analysis are largely congruent with current hypotheses. Zoraptera are not retrieved as close relatives of Acercaria. The monophyly of the entire lineage and of the major subgroups Psocodea, Phthiraptera, and Hemiptera is confirmed. Our data also support the monophyly of Auchenorrhycha and a sister-group relationship between Thysanoptera and Hemiptera (Condylognatha). In contrast to other lineages of insects, the hairy type of adhesive device is present only in one group within the Acercaria (Heteroptera, Cimicomorpha). The arolium is present in the groundplan but missing in several groups (e.g. Psocodea, Cicadoidea, Aphidoidea). Pretarsal pulvilli evolved several times independently. Tarsal euplantulae and different specialized clasping devices have evolved within Phthiraptera, whereas pretarsal attachment devices are missing in this ectoparasitic group. The potential to modify pretarsal attachment devices in their structural details has probably contributed to the very successful diversification of the predominantly phytophagous Hemiptera.

Introduction

Acercaria was introduced by Börner (1904) for a hemimetabolous lineage comprising "Psocoptera" (bark lice), Phthiraptera (true lice), Thysanoptera (thrips), and Hemiptera (bugs). Hennig (1969) considered Zoraptera (ground lice, angel insects) as its sister taxon and referred to the more inclusive lineage as Paraneoptera. Today, polyneopteran affinities of Zoraptera become more and more evident (e.g. Wheeler et al., 2001; Blanke et al., 2012; see also Trautwein et al., 2012); and Aceraria (e.g. Börner, 1904; Seeger, 1975; Kristensen, 1981) and Paraneoptera (e.g. Yoshizawa and Saigusa, 2001; Grimaldi and Engel, 2005) are used by different authors for the "hemipteroid assemblage". To avoid confusion we consistently use the former term, which is also less ambiguous.

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With more than 100 000 described species, Acercaria are an extremely diverse and successful lineage of insects. The group is characterized by a very broad spectrum of feeding habits. It comprises detritivores (mainly "Psocoptera"), highly specialized ectoparasites (Phthiraptera), miniaturized forms feeding on fungi or algae (Phlaeothripidae), numerous species feeding on plant saps (major part of Thysanoptera and Hemiptera), and also predators (which are restricted to several lineages of Heteroptera). Blood feeding on vertebrates evolved twice in Acercaria: once in Phthiraptera (Anoplura and Rhynchophthirina) and at least three times in Heteroptera [Cimicidae, Reduviidae, and Rhyparochromidae (Schuh and Slater, 1995)]. Acercaria are also extremely versatile in their habitat choices. Numerous species move efficiently on plant surfaces (e.g. Gorb et al., 2001) but there are also highly specialized semiaquatic and aquatic lineages (Gerromorpha, Nepomorpha), groups specialized on leaf litter and soil or

subcortical habitats, and ectoparasites adapted to feathers or hairs of their warm-blooded vertebrate hosts (e.g. Weber, 1969; Grimaldi and Engel, 2005).

With the necessity to cope with a broad spectrum of different surfaces, a tremendous variety of attachment devices has evolved in Acercaria. Within the group, the structure and function of attachment devices have been investigated in detail for a few selected species, such as the planthopper *Lycorma delicatula* (Frantsevich et al., 2008), several aphids (e.g. Carver and White, 1971; Lees and Hardie, 1988; Dixon et al., 1990), the true bug *Pameridea roridulae* (Voigt and Gorb, 2008), and the head louse *Pediculus humanus* (Soler-Cruz and Martin-Mateo, 2009). Systematic investigations of the pretarsal and tibial structures of Reduviidae and Miridae (Heteroptera) have been carried out by Weirauch (2005, 2007) and Schuh (1976), respectively. For a summary of cimicomorphan attachment devices see Schuh et al. (2009).

So far, adhesive devices of basal representatives of the subgroups of Acercaria have received little attention. A comprehensive comparative study of pretarsal structures of all major lineages is still missing. Especially the subgroups of Sternorrhyncha and Psocoptera have been largely neglected. In most available studies only one representative of one of the four lineages of Sternorrhyncha was included, even though these groups are morphologically highly heterogeneous.

Information on the tarsal and pretarsal morphology of Acercaria is scattered in the literature. An additional problem is the inconsistent nomenclature. Some authors refer to any kind of pretarsal attachment structure as "arolium". For *Lygus hesperus* (Miridae), for instance, Shrestha et al. (2007) disregards the commonly used nomenclature (see e.g. Beutel and Gorb, 2001) and refers to the attachment structures as arolia. However, his figures show clearly that these paired structures are in fact pulvilli. Another inappropriate term that persists is "dorsal arolium" (e.g. Cobben, 1978; Schuh and Slater, 1995; Schuh and Polhemus, 2009) even though this structure is clearly not an attachment device, but a peg-like or trichoform structure, and most likely a sensillum (= dorsomedian sensillum after Weirauch, 2005).

The monophyly of Acercaria appears to be well supported by morphological characters (Hennig, 1969; Kristensen, 1981; Kristensen et al., 1991; Beutel and Gorb, 2001, 2006), even though it is frequently rejected by molecular data (e.g. Yoshizawa and Johnson, 2005; Ishiwata et al., 2011). The monophyly of the major subgroups Psocodea (parasitic Phthiraptera and free-living "Psocoptera"; Seeger, 1975; Rudolph and Knülle, 1982; Lyal, 1985) and Hemiptera (e.g. Kristensen, 1981; Cryan and Urban, 2012) is also well supported. A sister-group relationship between Liposcelididae and the true lice also appears well established based on morphological (Lyal, 1985) and molecular data (Yoshizawa and Johnson, 2003; Johnson et al., 2004). However, what is still disputed is the monophyly of the true lice (Amblycera, Ischnocera, Rhynchophthirina, and Anoplura) (Barker et al., 2003; small-subunit rDNA; Johnson et al., 2004; 18S rDNA), the placement of Thysanoptera (Condylognatha versus Micracercaria, e.g. Yoshizawa and Saigusa, 2001; see also Willmann and Dathe, 2005; Grimaldi and Engel, 2005), the interrelationships of the hemipteran subgroups, and the monophyly of Auchenorrhyncha (e.g. Campbell et al., 1995; Cryan and Urban, 2012).

Despite considerable recent progress in the phylogenetic investigation of Acercaria (e.g. Yoshizawa and Johnson, 2003; Johnson et al., 2004; Cryan and Urban, 2012), a phylogenetic study covering all major lineages and a broad spectrum of morphological characters was still wanting. It is one aim of this study to provide a character set allowing a formal analysis of acercarian relationships, independently of molecular data that are already available [e.g. Johnson et al., 2004 (focused on Phthiraptera); Cryan and Urban, 2012 (focused on Hemiptera)] or will be available in the near future (see the Acercaria subproject of 1KITE: www.1KITE.org). However, the main focus is on the evolution of attachment structures in Acercaria. Our goal is to describe and document the attachment devices of representatives of all the major lineages, and to develop an evolutionary scenario for the relevant structures based on a cladistic analysis of characters of all body parts (see Appendix 1). Taxa were chosen for their (presumably) basal phylogenetic position. All figures show the attachment structures of females. Future phylogenetic analyses based on extensive molecular data (transcriptomes; see www.1KITE.org) will provide a robust basis for testing the hypotheses presented in this study.

Methods

Scanning electron microscopy

For SEM (Philips XL30 ESEM; Fei, Eindhoven, The Netherlands), specimens were completely dehydrated with ethanol (100%) over several stages, dried at the critical point (Emitech K850; Emitech, Ashford, Kent, UK) or treated with HMDS (hexamethyldisilazane; Brown, 1993), sputter-coated with gold (Emitech K500; Emitech), and fixed on a rotatable specimen holder (Pohl, 2010). Scandium software (Soft Imaging System, Münster, Germany) was used to obtain high-resolution images.

Cladistic analysis

We analysed 118 characters of the head, thorax, abdomen, and attachment structures (of the midlegs)

of 25 representatives of Acercaria plus eight outgroup taxa. Winclada 1.00.08 (Nixon, 1999) was used to enter the data in a matrix, and NONA (Goloboff, 1999) and TNT (Goloboff et al., 2008) for calculating minimum length trees (Ratchet, search settings: 1000 replicates, characters nonadditive, nonweighted). Branch support values (Bremer, 1994) were calculated with the function implemented in TNT.

Glossary

The terms used here are in accordance with the definitions of Dashman (1953) and Beutel and Gorb (2001).

Arcus: elastic, U-shaped band that embraces the base of the arolium ventrally with its arms extending distally in the lateral walls on either side.

Arolium: median lobe between the claws of the pretarsus. It can be completely membraneous or at least partly sclerotized.

Auxiliae: lateral sclerites beneath the bases of the claws.

Claws: hollow, multicellular, movable structures that articulate dorsally at the distal end of the tarsus.

Empodium: median process between the pulvilli that arises from the distal end of the unguitractor plate, is spine-shaped or lobe-like, and is often similar in form to the pulvilli.

Euplantulae: flexible, pad-like structures without hairs on the ventral side of one or more tarsomeres.

Manubrium: elongate medial sclerite in the dorsobasal region of the arolium. It is articulated proximally on the end of the tarsus between the bases of the claws and by its narrowed distal end it is attached like a handle to the base of the arolium.

Parempodia: bristle-like or fleshy appendages of the distal part of the unguitractor plate.

Planta: distal part of an unguitractor plate, which is divided into two sclerites.

Pretarsus: terminal part of the hexapod leg, closely associated with the distal end of the terminal tarsomere.

Pulvilli: smooth or hairy paired lateral membraneous lobes ventral to the claws. They are located on the auxiliae, which participate in control of pulvillar movements.

Tarsus: distal part of a hexapod leg.

Unguitractor plate: median basal plate of the ventral surface of the pretarsus, to which the unguitractor apodeme is attached. It is usually invaginated into the end of the terminal tarsomere. Its surface is highly variable.

Taxa examined

Auchenorrhyncha.
Cicadomorpha: Cercopidae, *Philaenus spumarius* (L., 1758), *Cercopis vulnerata* (Rossi, 1807).
Cicadoidea: Cicadidae, *Cicadetta montana* Scopoli 1772.
Membracoidea: Membracidae, *Centrotus cornutus* (L., 1758). Cicadellidae, *Cicadella viridis* (L., 1758).
Fulgoromorpha: Cixiidae, *Cixius* sp., Delphacidae, *Javasella* sp., *Dictyophora europaea* (L. 1767).

Coleorrhyncha. Peloridiidae, *Hackeriella veitchi* (Hacker 1932).

Heteroptera.
Dipsocoromorpha: Dipsocoridae, *Ceratocombus australiensis* Gross, 1950, Schizopteridae, *Corixidea* sp.
Enicocephalomorpha: Enicocephalidae, *Systelloderes* sp.
Pentatomomorpha: Pentatomidae, *Graphosoma lineatum* (L., 1758), *Pentatoma rufipes* (L., 1758).

Psocodea

Phthiraptera.
Amblycera: Menoponidae, *Trinoton anserinum* [Fabricius (J.C.), 1805].
Anoplura: Pediculidae, *Pediculus humanus capitis* L., 1758, *Pediculus humaus corporis* L., 1758; *Phthirus pubis* L., 1758.
Ischnocera: Trichodectidae, *Trichodectes melis* [Fabricius (J.C.), 1805]; Philopteridae, *Columbicola* sp.
Rhynchophthirina: Haematomyzidae, *Haematomyzus elephantis* (Piaget, 1869).

Psocoptera.
Psocomorpha: Caeciliidae, *Caecilius flavidus* (Stephens, 1830).
Troctomorpha: Liposcelididae, *Liposcelis* sp., *Embidiopsocus* sp.
Trogiomorpha, Trogidae, *Cerobasis* sp.

Sternorrhyncha

Aleyrodoidea: Aleyrodidae, *Aleyrodes* sp.
Aphidoidea: Drepanosiphidae, *Drepanosiphum plantanoides* (Schrank, 1801); Aphididae, *Microsiphum* sp.
Coccoidea: Pseudococcidae, *Pseudococcus* sp; Coccidae, *Coccus* sp.
Psylloidea: Psyllidae, *Cacopsylla* sp.

Thysanoptera

Terebrantia: Thripidae, *Frankliniella* sp.

Zoraptera

Zorotypidae: *Zorotypus weidneri* New, 1978.

Outgroups

Hymenoptera, Xyelidae: *Xyela* sp.
Neuroptera, Nevrorthidae, *Nevrorthus* sp.
Orthoptera, Caelifera, Acridiidae: *Locusta migratoria* (L., 1758).
Orthoptera, Ensifera, Tettigoniidae: *Tettigonia viridissima* (L., 1758).
Odonata, Gomphidae, *Ictinus angulosus selys*, 1854.
Plecoptera, Nemouridae, *Nemoura cinerea*, Latreille 1796.

Results

Tarsal morphology

Auchenorrhyncha (Figs 1 and 2). Fulgoromorpha, Cixiidae, and Delphacidae (Fig. 1c,j,k). The tarsi of all examined species are 3-segmented and an arolium (ar, Fig. 1c) is present. In delphacids two strong bristles (Weirauch, 2005: guard setae) are inserted dorsally on the distal part of the tarsus.

In *Cixius* sp. the distal tarsomere of the fore- and midlegs is slightly longer than the others, whereas in the hindleg the proximal tarsomere is almost three times as long as the two distal ones. The apices of the two basal segments each bear two thick bristles. The unguitractor plate of *Cixius* sp. (Fig. 1j) and *Javasella* sp. (Fig. 1k) is characterized by a washboard-like surface. It is subdivided into small sclerotized platelets in three columns and 16 rows in *Cixius* sp., whereas they are arranged in two columns and seven rows in *Javasella* sp.

Cicadomorpha

Membracoidea, Membracidae, and Cicadellidae (Fig. 1b,d,g,h). The tarsi are 3-segmented. The proximal segment is the smallest. The dorsal side of the pretarsus appears scaly. A bilobed arolium (bar, Fig. 1b,d) is present. The arolium is largely fused with the claws. Only the tip of the claw is free. The surface of the unguitractor plate appears scaly (Fig. 1g,h). In *Centrotus* the entire dorsolateral region of the pretarsus is strongly sclerotized (dls, Fig. 2c). Medially adjacent to this sclerotized area is a large plate-like sclerite (ms, Fig. 2c). A sensillum (sen, Fig. 1d) protrudes at the inner distal corner of this structure. No sclerites are present on the ventral side of the pretarsus.

In *Cicadella* the dorsolateral regions of the arolium are also heavily sclerotized. The medial sclerites (ms, Fig. 2d) are present, but triangular and much smaller than those of *Centrotus*. These sclerites also bear a sensillum (sen, Fig. 1b). The sensilla in *Cicadella viridis* appear more delicate than those of *Centrotus cornutus*.

Cicadoidea, Cicadidae (Fig. 1a). The tarsi are 3-segmented. No specific attachment structures are present in *Cicadetta montana*. A single sensillum is present between the claws. Whether this sensillum is homologous with the "dorsal arolium" of enicocephalids is unclear. Three thick bristles are arranged in a row on the ventral base of the claws. Ventrally the tarsomeres are densely covered with short setae. Additionally, a long and thin sensillum is present on the ventral side of the first and third tarsomere.

Cercopoidea, Cercopidae (Figs 1e,f and 2a,b). The tarsi are 3-segmented. An arolium is present. It is medially distinctly incised. A protrusion with a vestiture of microtrichia (mt, Fig. 1e,f) is present on the distolateral region of the arolium, directly below the claws. A sclerotized bar bearing 3–4 thick bristles (sb, Figs 1i and 2a) is present ventrolaterally of the arolium on each side of the pretarsus. Dorsally a long sclerite (dls, Fig. 2b) is directly adjacent to the claws. These dorsolateral sclerites enclose a V-shaped medial sclerite (ms, Fig. 2b). Three setae are inserted on each side of the distal part of the arms of the "V". There are no differences between the pretarsi of *Philaenus* and *Cercopis*.

Sternorrhyncha (Fig. 3)

Coccoidea, Pseudococcidae, and Coccidae. In *Pseudococcus* and *Coccus* the tarsus is composed of one segment (Fig. 3a). Only one claw is present. On each side of the base of the claw a capitate fleshy structure (termed "claw digitule" by Cockerell, 1893 and Kondo, 2006) is present. Dorsally two long, slender setae with capitate ends (= tarsal digitules, tadi) are present. The structure of the claw digitules strongly suggests that they are homologous with pulvilli.

Aphidoidea, Drepanosiphidae, and Aphididae. The tarsi are 2-segmented (Fig. 3b,c). An eversible, cushion-like pad (tip, Fig. 3b) is present between the tarsus and tibia in *Microsiphum* sp. and *Aphis sambuci*. Additionally, setiform parempodia are located on the pretarsus.The pad between tibia and tarsus is absent in *Drepanosiphum* sp., but fleshy pulvilli (referred to as "empodial pads" in Kennedy, 1986) are present (pu, Fig. 3c). There is no difference in the attachment structures between winged and wingless morphs. Some species of *Neophyllaphis* bear two eversible adhesive

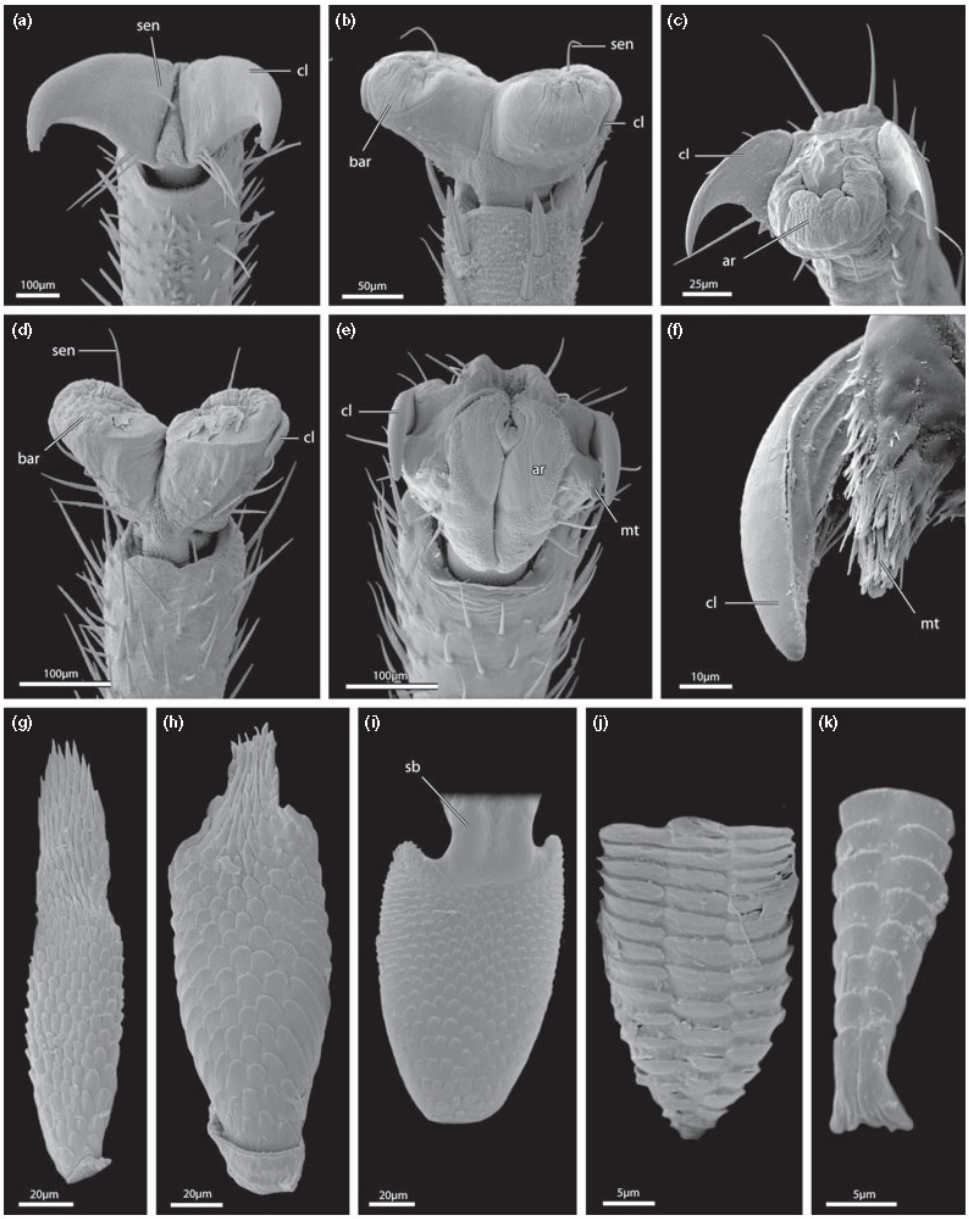

Fig. 1. Tarsi of Auchenorrhyncha. (a) *Cicadetta montana* (Cicadidae), ventral view. (b) *Cicadella viridis* (Cicadellidae), ventral view. (c) *Cixius* sp. (Cixiidae), frontal view. (d) *Centrotus cornutus* (Membracidae), ventral view. (e) *Cercopis vulnerata* (Cercopidae), ventral view. (f) *Cercopis vulnerata*, detail view of the protrusion covered in microtrichia. (g–k) unguitractor plates. (g) *Cicadella viridis*. (h) *Centrotus cornutus*. (i) *Cercopis vulnerata*. (j) *Cixius* sp. (k) *Javasella* sp. ar, arolium; bar, bilobed arolium; cl, claw; mt, microtrichia; sb, sclerotized bar; sen, sensillum.

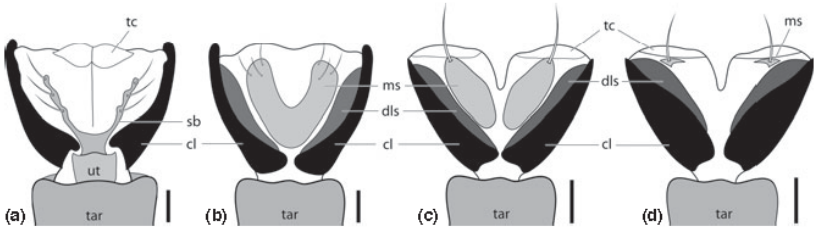

Fig. 2. Sclerites of pretarsi of Auchenorrhyncha. (a) *Cercopis vulnerata*, ventral view. (b) *Cercopis vulnerata*, dorsal view. (c) *Centrotus cornutus*, dorsal view. (d) *Cicadella viridis*, dorsal view. cl, claw; dls, dorsolateral sclerite; ms, medial sclerite; sb, sclerotized bar; tar, tarsus; tc, area of thickened cuticle; ut, unguitractor.

vesicles on the posterior abdominal sternites (Carver and White, 1971).

Psylloidea, Psyllidae. The tarsi of *Cacopsylla* are 2-segmented (Fig. 3d). A bilobed arolium (bar) is present. Three strong guard setae (gs) are present on the dorsal side of the tarsus. The distal part of the arolium is smooth, whereas the proximal part shows a rippled surface structure. Ventrally two setiform parempodia (par) arise from the unguitractor plate.

Aleyrodoidea, Aleyrodidae. The tarsi of the examined species are 2-segemented and covered with small wax platelets like the rest of the body (Fig. 3e). Dorsally one long guard seta is present. The two claws are largely covered with microtrichia from their bases to the middle region. They are thin and their tip remains glabrous. Between them a spine-like empodium (em) approximately as long as the claws is present. The base of this structure is also covered with microtrichia. The tip is flattened and glabrous with lamellae.

Most authors follow Quaintance and Baker (1913) in referring to this medial structure as "paronychium." However, Deshpande (1933) suggested to "treat the paronychium as an empodium rather than as a pulvillus".

Heteropterodea (Fig. 4)

Coleorrhyncha, Peloridiidae. The tarsi of *Hackeriella* are 2-segmented (Fig. 4c). An arolium is present between the claws.

Enicocephalomorpha. The tarsi are 2-segmented in *Systelloderes* (Fig. 4a,f). The distal tarsomere is about four times longer than the proximal one, and densely covered with long setae on all sides. There are no specific attachment structures. Two setiform parempodia (par, Fig. 4a) arise from the distal part of the unguitractor plate (ut). An alveolus is not recognizable. The unguitractor plate bears rectangular scales on its lateral side. The ventral distal rim of the distal tarsomere bears a row of microtrichia (= ventral brush after Weirauch, 2005). Dorsally between the claws, a so called "dorsal arolium" (ds, Fig. 4f) is present. This name is misleading as the structure is clearly not an arolium, but a sensillum (= dorsomedian sensillum after Weirauch, 2005). The foreleg in enicocephalids is distinctly modified for capturing prey. The tarsus comprises only one segment, and the distal part of the tibia bears an armature consisting of spiniform setae.

Dipsocoromorpha, Dipsocoridae, and Schizopteridae. The tarsi are 2-segmented in the species examined (Fig. 4b). The distal tarsomere is about three times longer than the proximal one. No specific pretarsal attachment structures are present in *Ceratocombus australiensis*. The lateral part of the unguitractor plate bears rectangular ridges. A ventral brush and setiform parempodia are missing, but two minute protuberances are present at the distal part of the unguitractor plate where the parempodia normally arise. These structures probably represent strongly reduced parempodia. It is very unlikely that this is an artifact as the same condition is found on all legs and a line of fracture is never recognizable. In the males of *Corixidea* there is an arolium present on the midlegs. There are no parempodia present on the midlegs, only on the hind- and forelegs. According to Stys (1983), metacoxal adhesive pads are present in Dipsocoromorphs. However, they were absent in all species examined.

Pentatomomorpha, Pentatomidae. The tarsi are 3-segmented in pentatomids (Fig. 4d,e). The ventral distal rim of the distal tarsomere bears a row of microtrichia, referred to as ventral brush (Weirauch, 2005). A small seta is present at the lateral end of the row. Two long setiform parempodia (par, Fig. 4d) arise from an alveolus on the distal part of the unguitractor plate. The ventral and lateral surfaces of the unguitractor plate bear distinct ridges. Large pulvilli (pu, Fig. 4d) are present. Their dorsal side is lamellate (Fig. 4e) and the ventral side more or less concave (variable among species).

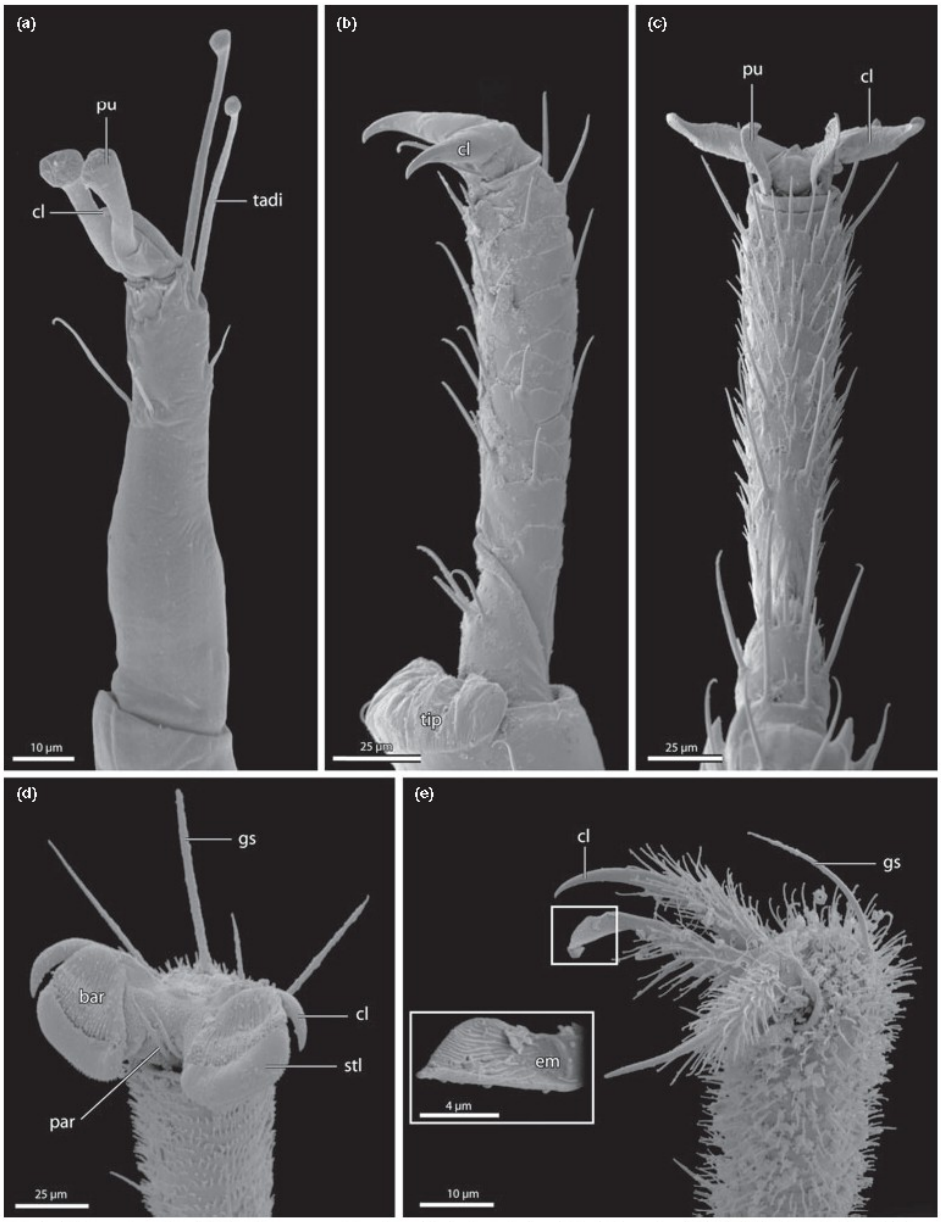

Fig. 3. Tarsi of Sternorrhyncha. (a) *Pseudococcus* sp. (Pseudococcidae), lateral view. (b) *Aphis sambuci* (Aphididae), lateral view. (c) *Drepanosiphum* sp. (Drepanosiphidae), ventral view. (d) *Cacopsylla* sp. (Psyllidae), frontal view. (e) *Aleyrodes* sp. (Aleyrodidae), lateral view. bar, bilobed arolium; cl, claw; em, empodium; gs, guard seta; par, parempodia; pu, pulvillus; stl, sticky lip of the arolium; tadi, tarsal digitules; tar, tarsus; ti, tibia; tip, tibial pad.

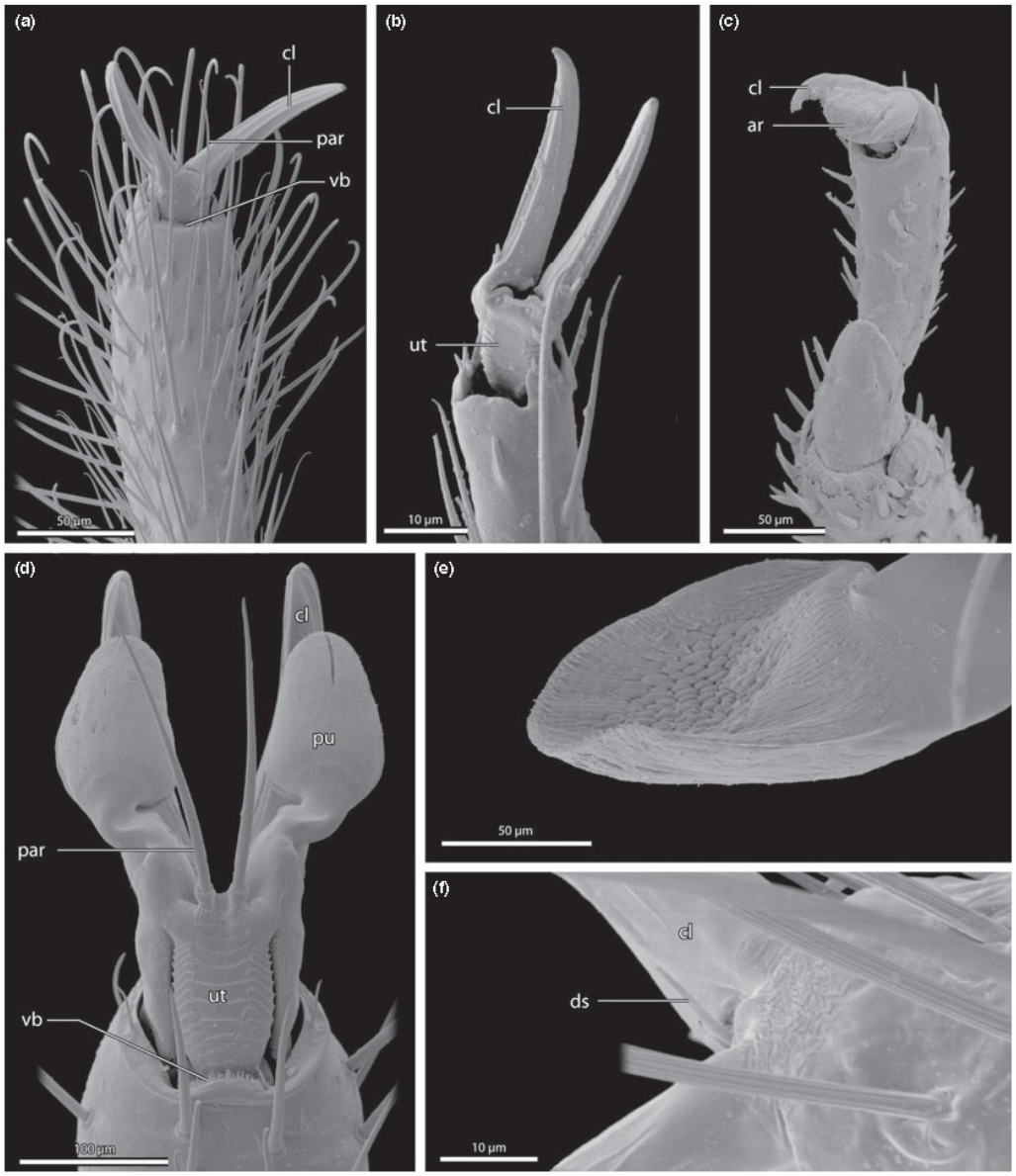

Fig. 4. Tarsi of Heteropterodea. (a) *Systelloderes* sp. (Enicocephalidae), ventral view. (b) *Ceratocombus australiensis* (Dipsocoridae), ventrolateral view. (c) *Hackeriella veitchi* (Peloridiidae), ventrolateral view. (d) *Graphosoma lineatum* (Pentatomidae), ventral view. (e) *Graphosoma lineatum* (Pentatomidae), dorsal surface of the pulvillus. (f) *Systelloderes* sp. (Enicocephalidae), dorsal view of the pretarsus. ar, arolium; cl, claw; ds, dorsal sensillum; par, parempodia; pu, pulvillus; ut, unguitractor; vb, ventral brush.

Psocodea (Fig. 5)

Troctomorpha, Liposcelididae. The tarsi are 3-segmented in *Liposcelis* (Fig. 5a). Adhesive structures are absent. The claws are serrate. The femur is distinctly enlarged. All tarsomeres, as well as the lateral and dorsal sides of the claws, are densely covered with microtrichia.

Psocomorpha, Caecilidae. The tarsi are 2-segmented in *Caecilius* (Fig. 5b). Paired, flap-like pulvilli are present. Two guard setae are inserted on the dorsal side of the distal tarsal segment.

Trogiomorpha, Trogidae (Fig. 5c). Tarsi are 2-segmented in *Cerobasis*. Paired fleshy pulvilli are present. Two smooth claws are present (in other species claw teeth may be present, Yoshizawa, 2005). Three long, strong guard setae are located on the dorsal side of the distal tarsal segment. Directly proximad the pulvilli additional adhesive hairs (adh, Fig. 5c) are present [called "Basalhaare" in Weidner (1972, p. 50)]. They arise from the claws, not from the unguitractor plate.

Amblycera, Menoponidae. The tarsi are 2-segmented in *Trinoton* (Fig. 5d,g). The proximal tarsomere is smaller than the distal one and both bear smooth, slightly concave euplantulae (eu, Fig. 5d). The proximal surface of the euplantulae is covered with tubercles (tu, Fig. 5g). Two sensilla with a flag-like appearance (sen, Fig. 5d) are located at the ventral base of the proximal tarsomere. Two claws are present.

Ischnocera, Trichodectidae, and Philopteridae. The tarsus is 1-segmented and only one claw is present in *Trichodectes melis* (Trichodectidae) (Fig. 5e). Three to five stout, cone-like hyaline structures (hyc) are present on the apex of the tibia. In ischnoceran species parasitizing birds (*Columbicola* sp., Philopteridae), two claws are present.

Anophura, Pediculidae. The tarsus is 1-segmented and only one large claw is present (Fig. 5f). A thumb-like process (thp) is present at the distal part of the tibia. It is opposed to the claw and combined, both structures enclose the hairshaft of the host. At the ventral side of the tarsus a round, pad-like euplantula (eu) is present. A claw-shaped apophysis (apo) arises from it. At the base of the claw a fingerlike process, possibly with sensory function (Soler-Cruz and Martin-Mateo, 2009), is present.

Rhynchophthirina, Haematomyzidae. The tarsus is 1-segmented (Fig. 5h). There is one main claw, and directly above is a smaller accessory claw ("Nebenkralle" after Weber, 1969). The accessory claw (acl) is present only on the mid- and hindlegs. No specific attachment structures are present.

Thysanoptera, Terebrantia, Aeolothripidae. The tarsi are 2-segmented in *Frankliniella* (Fig. 6a,b). An eversible, balloon-shaped pretarsal structure is a modified arolium (ar, Fig. 6b). In retracted condition it is encased by two spoon-shaped valves (va, Fig. 6a). Those valves are reduced claws (see Heming, 1971a, 1971b). Distally these valves are covered with tooth-like microtrichia (mt).

Character coding of tarsal structures (for character coding of other structures, see Appendix 2)

Coding as (0) or (1) does not imply a priori polarity assessment. We do not follow the convention of coding presumably plesiomorphic characters as (0). We consistently coded the adhesive structures of the middle leg.

99. Parempodia on unguitractor plate: (0) absent; (1) elongate and setiform, inserted in an alveolus.

100. Number of tarsal segments: (0) one; (1) two; (2) three; (3) more than three.

101. Arolium: (0) absent; (1) present; (2) eversible; (3) bilobed.

102. Sticky terminal lip of arolium: (0) absent; (1) present.

103. Pulvilli: (0) absent; (1) present.

104. Euplantulae: (0) absent, (1) present.

105. Number of claws: (0) one; (1) two; (2) reduced; (3) main claw plus accessory claw.

106. Claw teeth: (0) absent; (1) present.

107. Protuberance with microtrichia on distolateral side of the pretarsus: (0) absent; (1) present.

108. Sensorial setae on mesal side of arolium: (0) absent; (1) present.

109. Adhesive claw setae: (0) absent; (1) present.

110. Eversible structure between tibia and tarsus: (0) absent; (1) present.

111. Tibial thumb-like process: (0) absent; (1) present.

112. Empodial paronychium: (0) absent; (1) present.

113. Tarsal apophysis on the ventral side of the tarsus: (0) absent; (1) present.

114. Two dorsal capitate setae: (0) absent; (1) present.

115. Flag-like sensilla on the 1st tarsal segment: (0) absent; (1) present.

116. Fingerlike process below claw: (0) absent; (1) present.

117. Ventral brush: (0) absent; (1) present.

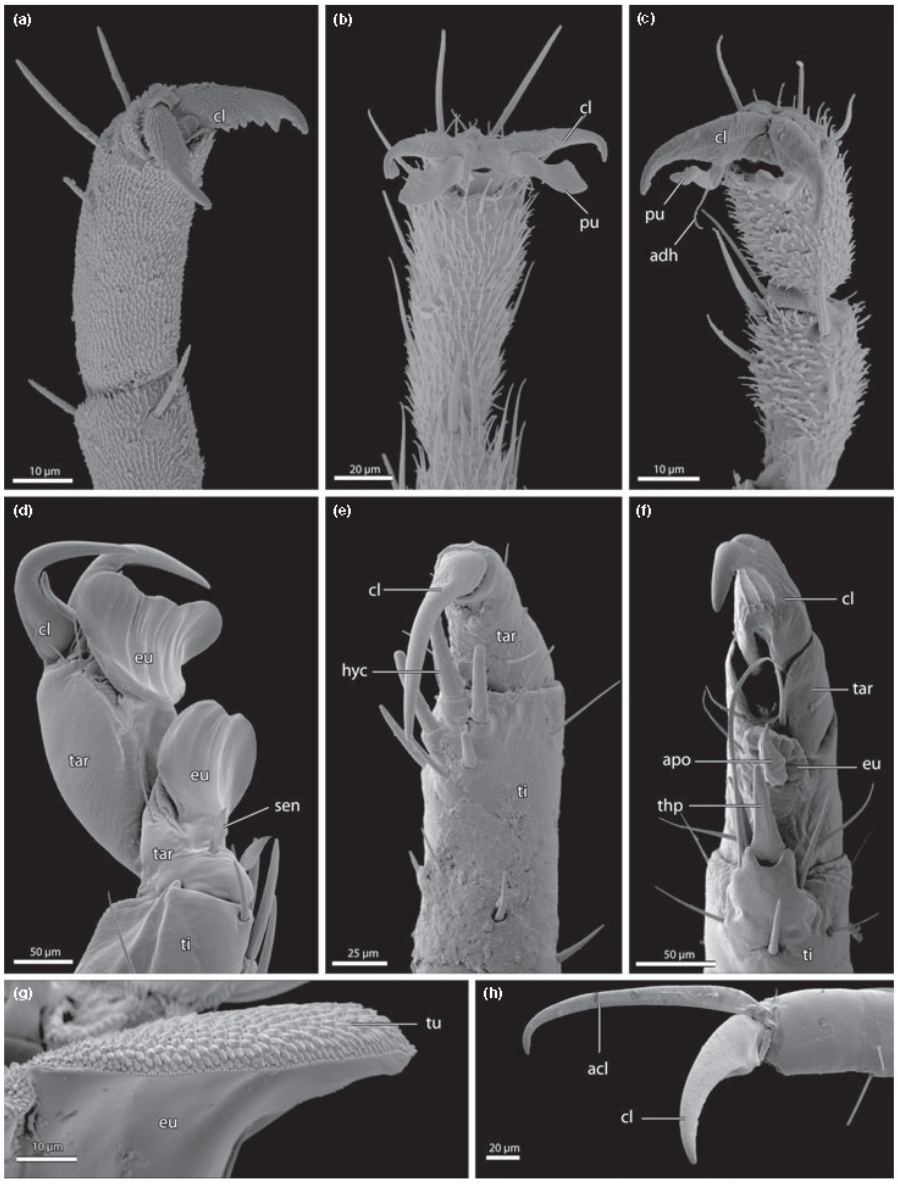

Fig. 5. Tarsi of Psocodea. (a) *Embiopsocus* sp. (Troctomorpha, Liposcelididae), lateral view. (b) *Caecilius flavidus* (Psocomorpha, Caeciliidae), ventral view. (c) *Cerobasis* sp. (Trogiomorpha, Trogidae), ventral view. (d) *Trinoton anserinum* (Amblycera, Menoponidae), lateral view. (e) *Trichodectes melis* (Ischnocera, Trichodectidae), ventral view. (f) *Pediculus humanus* (Anoplura, Pediculidae), ventral view. (g) *Trinoton anserinum* (Amblycera, Menoponidae), detail of the dorsal surface of the euplantulae. (h) *Haematomyzus elephantis* (Rhynchophthirina, Haematomyzidae), lateral view. acl, accessory claw; adh, adhesive hair; apo, apophysis of the euplantulum; cl, claw; eu, euplantulae; hyc, hyaline cones; pu, pulvillus; tar, tarsus; thp, thornlike process; ti, tibia; tu, Tubercle.

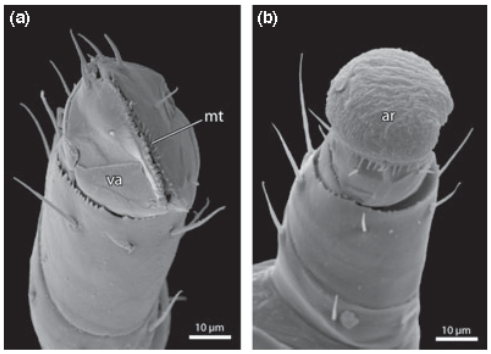

Fig. 6. Tarsi of Thysanoptera. (a) *Frankliniella* sp. Valves closed around the resting arolium. (b) *Frankliniella* sp. Arolium fully extended. ar, arolium; mt, microtrichia; va, valves.

Cladistic analysis

The analysis of 118 characters yielded three most parsimonious trees (195 steps, Ci: 68, Ri: 84). The strict consensus tree is shown in Fig. 7. Adhesive pad characters are mapped on the tree in Fig. 8. Apomorphies of ingroup taxa (character optimization: unambiguous) are listed in the following. Homoplasious changes are in italics. Further information about the characters can be found in Appendix 1 and 2.

Acercaria [Bremer support (BS): 4]

Lacinia stylet-like (7/1), single complex formed by abdominal ganglia (12/2), anterior region of 2nd axillary sclerite inflated (26/1), *fusion of gonangulum with tergum IX (44/1)*, number of Malpighian tubules reduced (93/2), *two tarsal segments (100/1)*.

Psocodea (BS: 5)

Rupture-facilitating modification at base of antennal flagellum (0/1), cardo and stipes fused (4/2), cibarial water-vapour uptake apparatus (10/1), two axonemes in spermatozoa (43/2), *arolium absent (101/1)*.

Liposcelididae + True lice (BS: 4)

Head and body dorsoventrally flattened (86/1), *hind-femora enlarged (87/1)*, meso- and metanotum fused (88/1), *compound eyes reduced (89/1)*.

True lice ("Phthiraptera", BS: 2)

Number of antennal flagellomeres reduced (58/1), ovipositor simplified (80/1).

True lice excl. Amblycera (BS: 2)

Maxillary palps absent (41/1), broad basal apodeme (63/1) and partly fused ventral plates (64/1) of the male genitalia, *only one tarsal segment (100/0)*, *single claw (105/0)*.

Rhynchophthirina + Anoplura (BS: 5)

Mandible stylet-like (3/1), lacinia absent (5/0), *cibarial water-uptake apparatus absent (10/0)*, *articulations between the mesomere, anterodorsal extension of ventral plate and posterior end of basal plate of the genitalia absent(59/0)*, *mesomere of the aedeagus pointed posteriorly (66/1)*, posteromedian part of basal plate of male genitalia sclerotized (67/1), *proboscis present (77/2)*, pronotum and procoxae fused (83/1), anterior tentorial pits absent (84/1), *hind femora not enlarged (87/0)*.

"Condylognatha" (Hemiptera + Thysanoptera; BS: 1)

Mandibles stylet-like (3/1), distal median plate of forewing positioned next to second axillary sclerite and articulating along convex hinge (33/1), *maxillary palps absent or reduced to less than four segments (41/1)*, *proboscis present (77/2)*, dorsal shift of anterior tentorial pits (84/2), labrum narrowed (94/1).

Hemiptera (Auchenorrhyncha, Heteropterodea, and Sternorrhyncha; BS: 3)

Cardo absent (4/1), labial rostrum present (8/1), anterior axillary folding-line forked around distal end of second axillary sclerite, proximal branch running through distal portion of 2Ax (27/1), tubular labium comprising three segments (55/1).

Auchenorrhyncha (BS: 4)

Proximal median plate of the forewing membraneous (31/1), *Evan's organ present (73/1)*, complex tymbal acoustic system present (91/1), *antennal flagellum aristate (92/1)*, *three tarsal segments present (100/2)*.

Fulgoromorpha (BS: 4)

Tegulae enlarged with broad extension encircling entire margin (20/1), pretentorium unites internal extremities of mandibular lever and corpotentorium (45/1), sensory plate organs of pedicel present (72/1), *arolium with sticky terminal lip (102/1)*.

Cicadomorpha (Bremer support: 1)

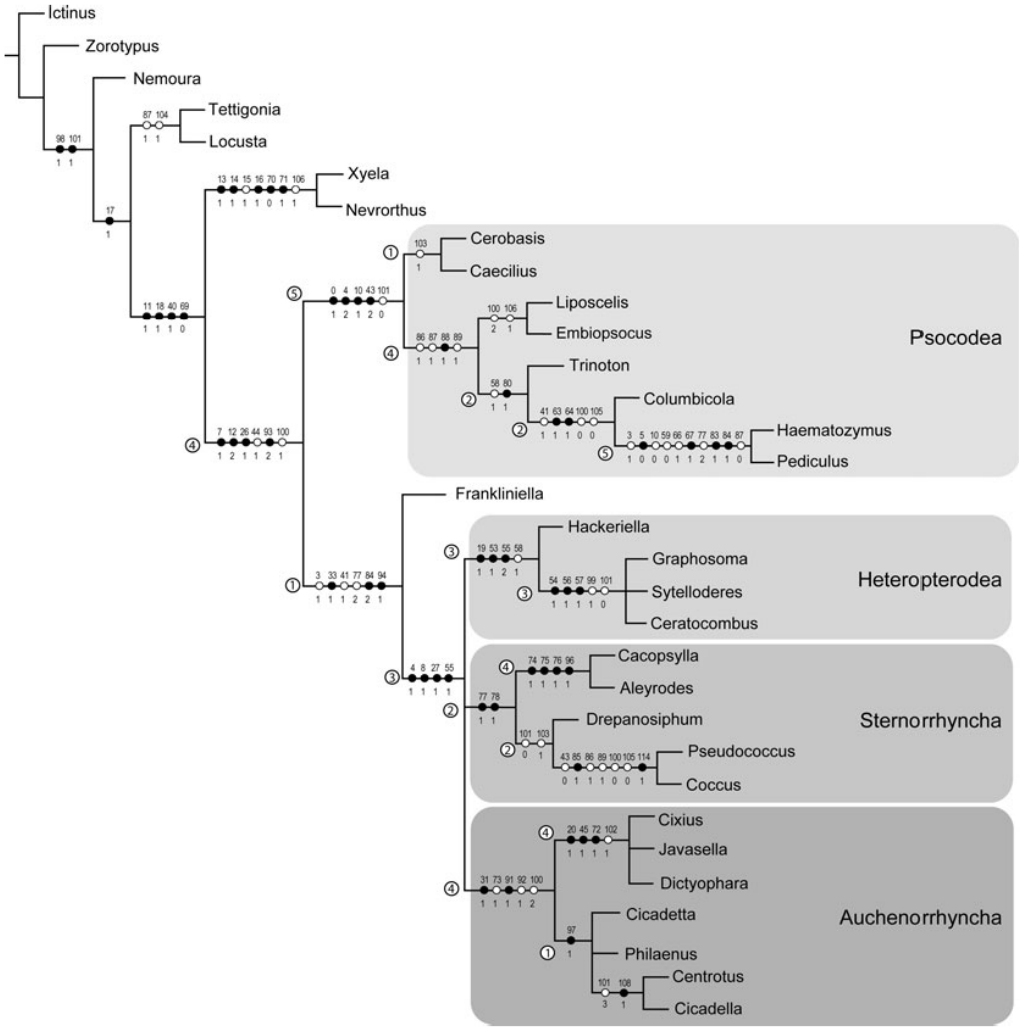

Fig. 7. Strict consensus cladogram of 118 characters (195 steps, Ci: 68, Ri: 84, unambiguous only). Black circles indicate non-homoplasious apomorphies, white circles homoplasious ones. Encircled numbers indicate Bremer Support values, which were calculated using TNT.

Gut with filter chamber containing Malpighian tubules (97/1).Heteropterodea (Coleorrhyncha + Heteroptera; BS: 3).

Tegulae of forewing absent (19/1), cephalic trichobothria (53/1), tubular labium comprising four segments (55/2), *number of flagellomeres of the antenna reduced (58/1).*

Heteroptera (BS: 3)

Metathoracic scent gland system (54/1), labial proboscis inserted anteriorly on head (56/1), dorsal abdominal glands present in immature stages(57/1), *parempodia on pretarsus present (99/1), arolium absent (101/0).*

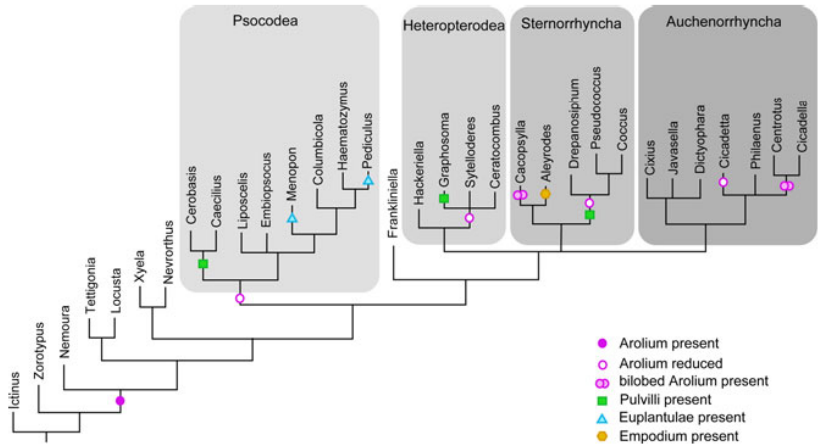

Fig. 8. Strict consensus cladogram of 118 characters, adhesive pad characters mapped on cladogram.

Sternorrhyncha (BS: 2)

Proboscis shifted posteriorly between procoxal bases (77/1), posterior parts of head capsule membraneous (78/1).

Psyllidae + Aleyrodidae (BS: 4)

Ductus ejaculatorius modified as sperm pump (74/1), abdomen narrowed by reduction of segments I and II (75/1), hind coxae broad and closely adjacent (76/1), eggs pedunculate (96/1).

Aphidoidea + Coccoidea (BS: 2)

Arolium absent (101/0), pulvilli present (103/1).

Discussion

Phylogenetic aspects

The phylogenetic relationships of Acercaria were discussed informally by Hennig (1969), in several review studies by Kristensen, 1981; Kristensen et al., 1991); and also briefly by Trautwein et al. (2012). The placement and phylogeny of the entire lineage were addressed in several studies based on molecular data sets (e.g. Wheeler et al., 2001; Kjer, 2004, 2006) and also the phylogenetic relationships of the subgroups (e.g. Wheeler et al., 1993; Yoshizawa and Johnson, 2010; Cryan and Urban, 2012). Aside from studies covering the entire Hexapoda (Beutel and Gorb, 2001, 2006), the first numerical analysis of morphological data including all orders of Acercaria was conducted by Yoshizawa and Saigusa (2001), based on characters of the base of the forewing. In the present study we attempt to compile and analyse a more extensive morphological data set, including characters of all body parts. In the following, the results of the analyses are compared with those obtained in earlier studies based on different data, and especially with respect to the evolution of attachment structures, the primary focus of this study.

Acercaria

The monophyly of Acercaria is well supported by our data set (Bremer support: 4). The Psocodea, Thysanoptera, and Hemiptera share a set of synapomorphic features of different body regions, such as a stylet-like lacinia, arguably a predisposition for specialized sucking piercing feeding habits, an inflated anterior region of the 2nd axillary sclerite, an extremely compacted abdominal ganglionic chain, and a reduced number of Malpighian tubules (shared with Holometabola excl. Hymenoptera; Beutel et al., 2011). The analysis based on our taxon sampling yielded a 2-segmented tarsus as an additional acercarian autapomorphy. This interpretation appears questionable as 3-segmented tarsi occur in several lineages [e.g. Psocoptera (partim), Heteroptera (majority of groups)]. Parallel loss of the 3rd tarsomere appears more plausible than a secondary acquisition in different groups. The slow optimization yielded strongly reduced labial palps and the absence of the abdominal sternite 1 as additional apomorphies of the Acercaria.

Our results do not support a placement of Zoraptera as the sister-group of Acercaria (e.g. Hennig, 1969; Beutel and Weide, 2005). The precise position of this

small and enigmatic order is not settled yet. However, there is an increasing consensus that they should be placed among the lower neopteran lineages (e.g. Kukalová-Peck and Peck, 1993; Wheeler et al., 2001; Yoshizawa and Johnson, 2005; Yoshizawa, 2007; Ishiwata et al., 2011; Yoshizawa, 2011; see also Trautwein et al., 2012).

The placement of Acercaria as sister-group of Holometabola is widely accepted even though poorly supported by morphological data (e.g. loss of larval ocelli; e.g. Beutel and Gorb, 2001, 2006). A clade including Acercaria and Holometabola (Eumetabola) is also tentatively supported by our data (with a very limited holomatabolan taxon sampling) and by molecular studies (e.g. Kjer, 2004; Ishiwata et al., 2011). However, this requires further confirmation. An arrangement with paraphyletic Acercaria and Psocodea as sister-group of Holometabola, as shown in Ishiwata et al. (2011), appears very unlikely considering the morphological evidence.

Psocodea

A clade Psocodea is well supported by unique morphological features (Figs 7 and 8; Rudolph and Knülle, 1982; Seeger, 1975) as well as molecular data (Murrell and Barker, 2005; Cryan and Urban, 2012; Ishiwata et al., 2011). A highly unusual apomorphic groundplan feature identified by Seeger (1975) is the cibarial water-uptake apparatus. An additional apomorphy probably present in the groundplan of Psocodea is the mortar-and-pestle apparatus of the cibarium (e.g. Tröster, 1990). It is still retained in the groundplan of Phthiraptera but is reduced in the majority of its subgroups (e.g. Tröster, 1990).

The relationships within Psocodea are still not fully clarified. However, a sister-group relationship between Liposcelididae and the true lice seems to be well supported by morphological characters such as enlarged hindfemora and fused pterothoracic nota (Figs 7 and 8; see also Lyal, 1985) and also by analyses of molecular data (Yoshizawa and Johnson, 2003; 12S, 16SrDNA). This renders the "Psocoptera" paraphyletic. The Phthiraptera (true lice) were weakly supported as a monophyletic unit (Bremer support: 2) in our analyses. Potential apomorphies are the reduced number of antennal flagellomeres, a condition also occuring in Heteroptera and Coleorrhyncha, and the simplified ovipositor (well developed in the psocodean groundplan). An entire series of apomorphies was suggested by Königsmann (1960), such as the absence of ocelli in all stages, the posteriorly tilted protocerebrum (see also Tröster, 1990), and a fusion of the metathoracic ganglion with the abdominal complex. Moreover, the complete reduction of the flight organs (absent or distinctly reduced in Liposcelididae), a dorsoventrally flattened body (also in Liposcelididae), and ectoparasitic habits were considered as obvious candidates for phthirapteran autapomorphies (see e.g. Grimaldi and Engel, 2005). Despite this seemingly strong morphological evidence, the monophyly of the true lice was questioned with respect to Amblycera in recent studies based on molecular data. Analyses of 18SrDNA (Johnson et al., 2004; Murrell and Barker, 2005) yielded a clade Amblycera + Liposcelididae on one hand, and the remaining true lice as its sister-group. This hypothesis suggests that parasitism in this lineage has evolved twice independently and also a series of features characterizing the four ectoparasitic groups. In an analysis using five different genes (nuclear 18S rDNA, Histone 3, wingless, mitochondrial 16S rDNA, and COI; Yoshizawa and Johnson, 2010) those result were supported. However, the results of the study by Murrell and Barker (2005) also include the unlikely paraphyly of Hemiptera and an unorthodox placement of Coleorrhyncha as sister-group of Auchenorrhyncha. Considering the morphological data and the specialized ectoparasitism on mammals and birds, we consider a clade Phthiraptera as more likely, but further confirmation by more extensive molecular data is required.

The branching pattern obtained within the true lice corresponds with the phylogenetic hypotheses suggested in earlier morphological studies (Lyal, 1985; Tröster, 1990) and a study based on 18SrRNA (Barker et al., 2003). The basal placement of Amblycera (Königsmann, 1960; Lyal, 1985; Tröster, 1990; see also Grimaldi and Engel, 2005) was confirmed in our analyses. Unambiguous synapomorphies of Ischnocera, Rhynchophthirina, and Anoplura (Fig. 7) are modifications of the male genital apparatus, i.e. the presence of broad basal apodemes and partly fused ventral plates. The sister-group relationship between Rhynchophthirina and Anoplura (e.g. Lyal, 1985; Tröster, 1990) is supported by an entire series of synapomorphies (Fig. 7) such as stylet-like mandibles (like in Hemiptera), loss of the lacinia, secondary absence of the cibarial water-uptake apparatus, the fusion of the procoxae with the pronotum, and the absence of anterior tentorial pits. Species of Anoplura and Rhynchophthirina feed exclusively on liquid, like the hemipterans. The food substrate is exclusively blood of birds or mammals in the former group, whereas this is a rare exception in the case of the Hemiptera (e.g. Cimicidae and some Reduviidae). The underlying structural modifications differ fundamentally in both lineages (Weber, 1929; Tröster, 1990).

Condylognatha

The placement of Thysanoptera is a matter of long-standing controversy (e.g. Kristensen et al., 1991). The characters we analysed support a clade Condylognatha

(Fig. 7; Bremer support 1), i.e. a sister-group relationship between Thysanoptera and Hemiptera. Potential synapomorphies include the stylet-like mandibles (right mandible vestigial in thrips), a specifically articulated distal median plate of the forewing, the reduction of the maxillary palps (absent in Hemiptera, fewer than four segments in thrips), and a dorsal shift of the anterior tentorial pits. The same result was obtained in several studies using different morphological character sets (e.g. Kristensen, 1981; Yoshizawa and Saigusa, 2001; Wheeler et al., 2001; : fig. 10; see also Hennig, 1969) and was also tentatively supported by molecular data analysed by Ishiwata et al. (2011). The alternative hypothesis, a clade Micracercaria (Thysanoptera + Psocodea), is suggested by the presence of an enlarged dorsal cibarial muscle with an unpaired median tendon (e.g. Willmann and Dathe, 2005). A sister-group relationship between Thysanoptera and Psocodea was also tentatively supported by analyses of 18S rDNA and 28S rDNA (Wheeler et al., 2001) and a study using seven gene regions (Cryan and Urban, 2012). As in the study of Ishiwata et al. (2011), the sampling of psocodeans and thrips was very limited in Cryan and Urban's (2012) study, which focused on hemipteran relationships. The results of Wheeler et al. (2001) have to be taken with caution. Neither the analyses of 18SrRNA nor those of 28SrRNA (Wheeler et al., 2001; : figs 13 and 14) supported a clade only containing the psocodean and thysanopteran terminals. Moreover, the analytical procedure (POY, simultaneous alignment and parsimony analyses) has been shown to be less reliable than other approaches (Kjer et al., 2007; Ogden and Rosenberg, 2007; Yoshizawa, 2010).

Hemiptera

There is no doubt about the monophyly of Hemiptera (Auchenorrhyncha, Heteropterodea, and Sternorrhyncha; e.g. Hennig, 1969; Kristensen, 1981; Kristensen et al., 1991). The most conspicuous autapomorphy is the characteristic labial rostrum, with reduced palps and endite lobes. This finding is clearly supported by our own data (Fig. 7) and also by molecular studies using different data sets and analytical approaches (Kjer, 2006; Ishiwata et al., 2011; Cryan and Urban, 2012). The paraphyly of Hemiptera and an unlikely sister-group relationship between Thysanoptera and Sternorrhyncha were suggested in a study based on SSUrDNA (Murrell and Barker, 2005). However, the focus was on the relationships within Psocodea, and the sampling of outgroups (in this case Thysanoptera and Hemiptera) was limited.

Our data turned out to be insufficient for resolving the interrelationships of the three hemipteran subgroups. Schuh (1979) suggested Sternorrhyncha as the sister-group of the remaining three lineages, thus rendering "Homoptera" paraphyletic. The same conclusion was reached by Popov (1981, palaeontological data), Zrzavy (1992, morphological and ecological data) and Cryan and Urban (2012, extensive molecular data). A taxon consisting of Heteropterodea (= Prosorrhyncha) and Auchenorrhnycha was referred to as Euhemiptera. This was also supported in several studies analysing different partial sequences of 18SrDNA (Campbell et al., 1995; Dohlen and Moran, 1995; Sorensen et al., 1995).

Auchenorrhyncha

A clade Auchenorrhyncha (Bremer support: 4) was well supported by our data (Figs 7 and 8). The presence of a complex tymbal acoustic system appears to be a convincing argument for this clade. Within the group, Fulgoromorpha were also clearly confirmed as a monophyletic unit (Bremer support: 4). The monophyly of Auchenorrhyncha was also supported by analyses of sequences of a broad array of genes (Urban and Cryan, 2007; 18S rDNA, 28S rDNA, Histone 3, Wingless) and in an even more extensive study using seven gene regions (Cryan and Urban, 2012; 18S rDNA, 28S rDNA, histone H3, histone 2A, wingless, cytochrome *c* oxidase I, NADH dehydrogenase subunit 4). However, it was challenged in other studies. A sister-group relationship between Cicadomorpha and Aphidoidea was suggested based on characters of the head capsule by Hamilton (1981), and a closer relationship between fulgorids and true bugs was proposed by von Dohlen and Moran (1995). The latter study was based only on 18SrRNA, and the taxon sampling was very limited, with only nine species of Auchenorrhyncha included. Similarities in the morphology and histology of the digestive tract of Fulgoromorpha and Heteroptera were pointed out by Goodchild (1966; for a summary see Forero, 2008), arguably a result of parallel evolution. A sister-group relationship between Cicadomorpha and Heteropterodea (Heteroptera + Coleorrhyncha) appears as a serious alternative to the monophyly of Auchenorrhyncha. This was suggested in an evaluation of combined paleontological, molecular, and morphological data (Bourgoin and Campbell, 2002) and also supported by a recent study based on transcriptomes (Letsch et al., 2012). Considering the conflicting hypotheses, the issue of the monophyly of Auchenorrhyncha should be considered an unsolved question.

Heteropterodea (= Prosorrhyncha, Coleorrhyncha + Heteroptera)

Coleorrhyncha are clearly placed as the sister-group to Heteroptera (Fig. 7; Bremer support: 3). The same

result was supported by Cryan and Urban (2012) and in other studies (Wheeler et al., 1993; Ouvrard et al., 2000; see also Schlee, 1969), and also by a detailed comparative study of head structures (Spangenberg et al., in press). Furthermore, the wing-coupling structure of moss bugs is very similar to that of Heteropterans (D'Urso, 1993). Considering the overwhelming evidence from different sources, previous placements of Coleorrhyncha as a subordinate group within Heteroptera (Breddin, 1897) or Auchenorrhyncha (China, 1962; Murrell and Barker, 2005) can be regarded as obsolete. Structural affinities of Coleorrhyncha and members of Auchenorrhyncha include features of the heart (occupying six abdominal segments and with six sets of alary muscles; Pendergrast, 1962) and the presence of an arolium. We assume that these similarities are either symplesiomorphic (e.g. arolium) or results of parallel evolution.

The monophyly of Heteroptera was clearly confirmed (Bremer support: 3), whereas the relationships within the group remained unresolved. This is mostly due to the very fragmentary knowledge of the morphology of supposedly basal groups such as Enicocephalomorpha and Dipsocoromorpha (Wheeler et al., 1993; Xie et al., 2008; summarized by Weirauch and Schuh, 2011). The basal branching events in Heteroptera are not yet fully clarified. A recent analysis of multiple genes yielded a basal position of Nepomorpha (Li et al., 2012). The position of Enicocephalomorpha and Dipsocoromorpha varied in the Li et al. (2012) study depending on the method applied (maximum likelihood versus maximum parsimony). The placement of Nepomorpha at the base of Heteroptera would be consistent with findings of Mahner (1993, p. 15ff), who considered the reduction of the tentorium as an autapomorphy of Heteroptera excl. Nepomorpha. The tentorium of enicocephalids is largely reduced (R. Spangenberg, pers. obs.), but the condition in dipsocoromorphans is not yet known. The fast optimization search yielded one additional apomorphy for the Heteroptera: the presence of a ventral brush on the ventral distal rim of the distal tarsomere. However, it is absent in the members of Dipsocoromorpha examined.

Sternorrhyncha

Sternorrhyncha were clearly confirmed as a clade (Fig. 7). Autapomorphies are the posterior shift of the proboscis between the procoxal bases and the membraneous posterior parts of the head capsule. A sister-group relationship between Psyllidae and Aleyrodidae (Psyllomorpha) was also well supported (Bremer support: 4), which is not surprising as most characters were taken from Schlee (1969), who proposed this hypothesis. Synapomorphies are the ductus ejaculatorius modified as a sperm pump, the constriction of the abdominal base, the broad and closely adjacent hind coxae, and the pedunculate eggs. The only potential synapomorphy of aphids and coccids is the loss of the arolium. However, the arolium is lost several times within Acercaria.

In several studies based on 18S rDNA (Campbell et al., 1995; Sorensen et al., 1995), Psyllidae were placed as the sister-group of the remaining Sternorrhyncha, and Aleyrodidae as the sister-group of a clade comprising of Aphidoidea and scale insects. The same relationships were inferred from DNA nucleotid sequence data from seven gene regions (Cryan and Urban, 2012). Whiteflies share at least some morphological features with aphids and scale insects, such as reduced wing venation, sedentary or sessile nymphs, and antennae reduced to six or fewer segments (e.g. Grimaldi and Engel, 2005). Apparently the interrelationships of the sternorrhynchan subgroups require further investigation.

Evolution of attachment structures

Despite a very broad spectrum of structural variations, there are only two basic designs of attachment pad on insect legs: hairy and smooth (Beutel and Gorb, 2001). Interestingly, hairy structures that occur in different lineages of Polyneoptera and Holometabola (Beutel and Gorb, 2001, 2006) are lacking on the tarsus and pretarsus of the acercarian subgroups. An interesting exception is the hairy fossula spongiosa in several subgroups of Cimicomorpha. This is the only case of a hairy pad in Acercaria and, apart from tibial elements of some specialized clasping devices of true lice, the only tibial attachment structure occurring in the entire Hexapoda. The exact function of the fossula spongiosa is still unclear. It is possibly a tool for capturing prey, or alternatively a device involved in locomotion (Weirauch, 2007). It was pointed out by Beutel and Gorb (2001) that the function of adhesive devices of insect legs is generally not restricted to attachment. Easy detachment is equally important to guarantee efficient locomotion on a specific substrate.

The location of different attachment devices within Acercaria varies considerably. They occur on the pretarsus as an unpaired pad-like arolium, as paired pulvilli, or as an unpaired sclerotized empodium; on the tarsus as smooth euplantulae; and (as noted above) even on the distal tibia as a fossula spongiosa. This and the incompletely resolved relationships within Hemiptera impede the reconstruction of the evolutionary pathways. However, it is noteworthy that pretarsal attachment structures are mainly present in the primarily phytophagous Hemipterans, whereas tarsal and tibial attachment devices occur mostly in the ectoparasitic lice (Phthiraptera). In these taxa they are essential

for anchoring on the hairs or feather shafts of the host.

Some groups lack attachment devices completely, for example the ground-dwelling Zoraptera (Beutel and Gorb, 2006). They are also absent in Enicocephalomorpha, female Dipsocoromorpha, Gerromorpha, Nepomorpha, Leptodomorpha, Rhynchophthirina, and Troctomorpha. With the exception of the ectoparasitic Rhynchophthirina and the semi-aquatic and aquatic Gerromorpha and Nepomorpha, all these taxa are ground-oriented and live in leaf litter, in microhabitats similar to those of the zorapterans. The elephant lice do not attach to hairs in the typical case, but stay directly on the skin surface or in skin creases (Fowler and Mikota, 2006; p. 458). Their main anchoring mechanism appears to be the proboscis, which is firmly embedded in the skin of the host (Weber, 1969).

Arolium

Arolia are widely spread within Acercaria and a groundplan feature of this lineage. They are generally present in the Auchenorrhyncha examined (with the exception of Cicadidae), in Coleorrhyncha, and in Thysanoptera. An arolium is also present in the males of the genus *Corixidea* and several other male members of the Schizopteridae (Emsley, 1969; p. 20). The females of Dipsocoromorpha lack specific adhesive structures. The distinctly bilobed arolium of membracids and leafhoppers (Membracidae and Cicadellidae; Figs 1b,d and 2c,d; and Psylloidea; Fig. 3d) has apparently evolved independently in these groups, as potential autapomorphies of these lineages. A unique and apparently autapomorphic feature is the eversible, balloon-like arolium of Thysanoptera. In its retracted position it is enclosed between two valves. This is not the case in fulgorids, where the arolium is also eversible to a certain degree (Frantsevich et al., 2008).

The arolium was considered as a potential autapomorphy of Neoptera by Beutel and Gorb (2001, 2006). However, whether the unpaired pretarsal attachment pads occurring in different insect lineages are homologous is questionable. The sclerotization of the arolium of sawflies (Gladun, 2008), for instance, is completely different from the pattern found in the arolia of members of Cicadomorpha. The sclerotized Y-shaped ridge on the ventral side of the arolium in cercopoids may represent strongly modified planta, but this would imply that the auxillae and the arcus are reduced. The V-shaped sclerite on the dorsal side of the pretarsus of cercopids could be a modified manubrium. However, this interpretation is also uncertain. Due to the uncertain assessment of homologies, it is presently not possible to decide whether the differences between arolia occurring in acercarian and holometabolan lineages are due to secondary modifications of substructures or to nonhomology of the unpaired pretarsal pads as a whole.

In contrast, there is little doubt that the unmodified arolium of cercopoids and the bilobed arolium in membracids are homologous. This is clearly indicated by specific conformities in the inner structure and sclerotization of these devices. In both cases, the cuticle is thickened and composed of branched chitinous rods. A modification characterizing the Membracoidea examined is the loss of the ventral Y-shaped sclerite. A characteristic feature of membracids is the division of the medial sclerite into two separate elements (ms, Fig. 2c). It is V-shaped but undivided in cercopoids. In cicadellids these sclerites are greatly reduced in size (ms, Fig. 2d), arguably an autapomorphy of the family.

The homology of the attachment device of whiteflies is still unclear. In this study we reluctantly label it as an empodium. Most authors, however, follow Quaintance and Baker (1913) in referring to this structure as "paronychium" (= arolium). An arolium is defined as a median hollow lobe of the pretarsus (Dashman, 1953; Beutel and Gorb, 2001). The structure in the Aleyrodidae examined is not hollow, but resembles a spine-like empodium with a flattened tip. Median empodia are usually covered with acanthae (Beutel and Gorb, 2001). This applies only to the base of the structure occurring in Aleyrodidae. This and the absence of empodia in related groups suggests that this is a de novo formation and autapomorphy, rather than a structure homologous to the empodia occurring in several holometabolan lineages (e.g. Diptera).

The results of our analysis suggest the secondary loss of the arolium in several lineages. This includes Heteroptera, Aphidoidea, Coccoidea, and Psocodea. In all these groups, arolia were apparently functionally replaced by other kinds of attachment device, in most cases by paired pulvilli. Considering the relationships indicated by our analysis (Fig. 8) and other studies, it appears that the loss of the arolium is an autapomorphy of each of the taxa listed above. However, as a complete reduction of this structure also occurs in many other insect lineages (Beutel and Gorb, 2001, 2006), this feature is of minor phylogenetic significance.

Pulvilli

Pulvilli have evolved at least twice independently within Acercaria—in Psocoptera and in the "higher" Heteroptera, respectively (Fig. 7). Interestingly, pretarsal or tarsal adhesive pads are absent in most of the presumably basal taxa of examined Heteroptera, the Enicocephalomorpha, the semi-aquatic and aquatic lineages Gerromorpha and Nepomorpha, and also in Saldidae (Leptopodomorpha), predaceous and ground-

dwelling bugs, and arguably the sister-group of the remaining secondarily terrestrial heteropteran lineages (Wheeler et al., 1993). An arolium is present in Coleorrhynchans and some male members of the Schizopteridae (Dipsocoromorpha), and this is certainly a groundplan condition in Heteropterodea (and Acercaria). The loss of this unpaired pretarsal pad is probably a groundplan feature and autapomorphy of Heteroptera. Interestingly, in the megadiverse heteropteran subgroups Pentatomomorpha (ca. 14 500 spp.) and Cimicomorpha (more than 20 000 spp., Weirauch and Schuh, 2011) a novel type of attachment device occurs: paired pretarsal pulvilli. The presence of these adhesive structures is arguably related to a close association between those bugs and plants. As noted above, pretarsal and tarsal adhesive devices are absent in saldids. There is, however, one noteworthy exception: a structure resembling an empodium, similar to that of whiteflies, occurs in the genus *Aepophilus*. Interestingly, this attachment device, considered as a "true" arolium by Cobben (1978, p. 114 ff), is present only in fifth-instar nymphs and is completely lacking in all other stages. However, a "dorsal arolium" occurs in the adults of *Aepophilus bonnairei* (Schuh and Polhemus, 1980) and other saldids. Therefore it seems likely that Cobben misinterpreted this structure. He also stated the presence of arolia in Gerromorpha. However, the structures he described rather resemble paired accessory claws, and they were absent in species of *Gerris* we examined.

Pulvilli are also present in aphids and coccoids, apparently a result of parallel evolution. The pulvilli of coccoids are usually fleshy and thick, and therefore similar to those of the pentatomids examined. In contrast, the pulvilli of aphids are flattened like those found in trogiomorphs and psocomorphs (Psocodea). The shape of pulvilli can be very variable. This is particularly obvious in the Miridae (Schuh, 1976). However, the characteristic thickened cuticle with chitinous rods found in arolia is absent in the pulvilli examined.

Euplantulae and tibial pads

Within Phthiraptera no pretarsal attachment structures occur. The complete reduction of the arolium is probably related to ectoparasitic habits and a potential autapomophy of true lice. Within the group, different tarsal and tibial devices have evolved. A specific type of euplantulae is present in amblycerans, especially in species specialized on birds as hosts. They occur on both tarsomeres in Menoponidae, but only on the proximal segment in Laemobothriidae. Interestingly, euplantulae of the proximal tarsomere are also present in species of the genus *Paraheterodoxus* (Boopidae) (Marshall, 2003), even though these amblycerans live not on birds, but in the fur of the rufous rat-kangaroo. This is an example of how attachment devices of the same type can adapt to different surfaces or structures.

In Ischnocera and Amblycera the mandibles appear to play a more important role as grasping devices than the specialized structures on the legs (Bush et al., 2006). In specimens preserved in ethanol we observed that the hair shaft was not in contact with the legs any more, but was still firmly anchored between the mouthparts. In anoplurans the thumb-like process on the distal part of the tibia and the opposing claw enclose the hair. It is plausible to assume that the grasping mechanism is enhanced by the tarsal euplantulae. The same function is conceivable for the thick hyaline cones on the apex of the tibia in the Ischnocera examined. These cones on the tibial apex are apparently typical for many ischnoceran species specialized on birds (Smith, 2001).

Conclusions

As pointed out by Beutel and Gorb (2001), attachment devices can provide phylogenetic information despite functional constraints. In our study, the impact on the branching pattern was limited to an improved resolution within Psocodea. However, additional apomorphies of adhesive devices strengthened the support for different lineages (Psocodea, Fulgoromorpha, Heteroptera). Linked with a remarkable versatility in habitat choice, a very wide spectrum of attachment devices has evolved in Acercaria, with the notable exception of hairy pretarsal adhesive structures. Several acercarian subgroups can be characterized by features of the distal leg elements related to attachment and efficient locomotion on different substrates. The phylogenetic hypothesis presented here was based on a relatively limited character system and taxon sampling. In the near future, an extensive molecular data set will probably provide a robust phylogenetic framework for Acercaria and other hexapod lineages (see www.1KITE.org). This will be an ideal basis for reconstructing the evolution of attachment structures and other character systems.

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Appendix 1

Character state matrix

(?) Refer to missing character states; (–) refer to inapplicable characters.

	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Ictinus	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?
Nemoura	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tettigonia	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	?	?	?	?	?
Locusta	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	?	?	?	?	?
Xyela	0	0	0	0	0	1	0	0	0	1	0	1	0	1	1	1	1	1	1	0	?	1	?	?	?
Nevrorthus	0	0	0	0	0	1	0	0	0	1	0	1	0	1	1	1	1	1	1	0	?	?	?	?	?
Zorotypus	0	0	0	0	0	1	0	0	0	1	0	?	1	0	0	0	0	0	0	0	0	0	?	?	?
Trogiomorpha	1	0	0	0	2	1	1	1	0	0	1	1	2	0	0	0	0	1	1	0	0	0	1	1	0
Liposcelis	1	?	0	0	2	1	1	1	0	0	1	1	2	0	0	0	0	1	1	0	0	0	1	1	0
Embidiopsocus	1	?	0	0	2	1	1	1	0	0	1	1	2	0	0	0	0	1	1	?	?	?	?	?	?
Caecilius	1	0	0	0	2	1	1	1	0	0	1	1	2	0	0	0	0	1	1	0	0	0	1	1	0
Trinoton	1	0	0	0	2	1	1	1	0	0	1	–	2	0	–	0	0	1	1	–	–	–	–	–	–
Trichodectes	1	0	0	0	2	1	1	1	0	0	1	–	2	0	–	0	0	1	1	–	–	–	–	–	–
Haematomyzus	1	?	0	1	2	0	–	–	0	0	0	–	2	0	–	0	0	1	1	–	–	–	–	–	–
Pediculus	1	?	0	1	2	0	–	–	0	0	0	–	2	0	–	0	0	1	1	–	–	–	–	–	–
Frankliniella	0	1	1	1	0	1	0	1	0	1	0	1	2	0	0	0	0	1	1	0	0	1	1	2	1
Cacopsylla	0	2	0	1	1	1	1	1	1	0	0	1	2	0	0	0	0	1	1	0	0	0	1	2	0
Aleyrodes	0	2	0	1	1	1	1	1	1	0	0	1	2	0	0	0	0	1	1	?	?	?	?	?	?
Drepanosiphum	0	2	0	1	1	1	1	1	1	0	0	1	2	0	0	0	0	1	1	0	0	0	1	2	0
Pseudococcus	0	2	0	1	1	1	1	1	1	0	0	1	2	0	0	0	0	1	1	?	?	?	?	?	?
Coccus	0	2	0	1	1	1	1	1	1	0	0	1	2	0	0	0	0	1	1	?	?	?	?	?	?
Centrotus	0	2	0	1	1	1	1	1	1	0	0	1	2	0	0	0	0	1	1	0	0	0	1	2	0
Cicadella	0	2	0	1	1	1	1	1	1	0	0	1	2	0	0	0	0	1	1	0	0	0	1	2	0
Cicadetta	0	2	0	1	1	1	1	1	1	0	0	1	2	0	0	0	0	1	1	0	0	0	1	2	0
Cercopis	0	2	0	1	1	1	1	1	1	0	0	1	2	0	0	0	0	1	1	0	0	0	1	2	0
Cixius	0	2	0	1	1	1	1	1	1	0	0	1	2	0	0	0	0	1	1	0	1	0	1	2	0
Javasella	0	2	0	1	1	1	1	1	1	0	0	1	2	0	0	0	0	1	1	0	1	0	1	2	0
Dictyophora	0	2	0	1	1	1	1	1	1	0	0	1	2	0	0	0	0	1	1	0	1	0	1	2	0
Pentatomorpha	0	2	0	1	1	1	1	1	1	0	0	1	2	0	0	0	0	1	1	1	–	–	1	2	0
Systellonderes	0	2	0	1	1	1	1	1	1	0	0	1	2	0	0	0	0	1	1	1	–	–	1	2	0
Ceratocombus	0	2	0	1	1	1	1	1	1	0	0	1	2	0	0	0	0	1	1	1	–	–	?	?	?
Hackeriella	0	2	0	1	1	1	1	1	1	0	0	1	2	0	0	0	0	1	1	1	–	–	?	?	?

	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49
Ictinus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	1	1	0	0	0	0	?
Nemoura	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	1	1	0	0	0	0	0	?
Tettigonia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	1	0	0	0	0	0	?
Locusta	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	1	0	0	0	0	0	?
Xyela	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	0	1	0	0	0	0	0	?
Nevrorthus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	0	1	0	?	?	0	0	?
Zorotypus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	3	0	0	1	0	0	0	1	0	?
Trogiomorpha	1	1	0	1	1	1	0	1	0	0	1	0	0	1	1	1	0	1	2	1	0	?	?	0	?
Liposcelis	1	1	0	1	1	1	0	1	0	0	1	0	0	1	1	1	0	1	2	1	0	0	0	0	?
Embidiopsocus	?	?	?	?	?	?	0	?	?	?	?	?	?	?	1	1	0	1	2	1	0	0	0	0	?
Caecilius	1	1	0	1	1	1	0	1	0	0	1	0	0	1	1	1	0	1	?	1	0	0	0	0	?
Trinoton	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	0	1	?	?	0	1	0	0	?
Trichodectes	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	1	1	2	?	0	1	0	0	?
Haematomyzus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	1	1	?	?	0	0	0	0	?
Pediculus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	1	1	2	?	0	0	0	0	?
Frankliniella	0	1	0	1	1	1	0	?	1	1	1	1	1	1	0	3	1	0	3	1	0	0	0	?	?
Cacopsylla	1	1	1	1	1	1	0	1	1	0	1	0	0	1	0	2	1	1	1	1	0	0	0	?	?
Aleyrodes	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	2	1	1	0	1	?	?	0	?	?
Drepanosiphum	1	1	1	1	1	1	0	1	1	0	1	0	0	1	0	2	1	1	1	1	0	0	0	0	?
Pseudococcus	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	2	1	1	0	1	?	?	?	?	?
Coccus	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	2	1	1	0	1	?	?	?	?	?
Centrotus	1	1	1	1	1	1	1	1	1	0	1	0	0	?	0	2	1	1	1	1	0	0	0	0	?

(*Continued*)

	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49
Cicadella	1	1	1	1	1	1	1	1	1	0	1	0	0	?	0	2	1	1	1	1	0	0	0	0	?
Cicadetta	1	1	1	1	1	1	1	1	1	0	1	0	0	?	0	2	1	1	1	1	0	0	0	0	?
Cercopis	1	1	1	1	1	1	1	1	1	0	1	0	0	?	0	2	1	1	1	1	0	0	0	0	?
Cixius	1	1	1	1	1	1	1	1	1	0	1	0	0	?	0	2	1	1	1	1	1	0	0	0	?
Javasella	1	1	1	1	1	1	1	1	1	0	1	0	0	?	0	2	1	1	1	1	1	0	0	0	?
Dictyophora	1	1	1	1	1	1	1	1	1	0	1	0	0	?	0	2	1	1	1	1	1	0	0	0	?
Pentatomorpha	1	1	1	1	1	1	0	1	1	0	1	1	0	1	0	2	1	1	1	1	0	?	0	1	1
Systelloderes	1	1	1	1	1	1	0	1	1	0	1	0	0	1	0	2	1	1	?	?	0	0	0	0	0
Ceratocombus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	2	1	1	?	?	0	0	0	0	?
Hackeriella	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	2	1	1	?	1	0	0	0	0	?

	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74
Ictinus	?	?	0	0	0	0	–	0	1	?	?	?	?	?	?	?	?	?	?	1	1	0	0	–	0
Nemoura	?	?	0	0	0	0	–	0	0	?	?	?	?	?	?	?	?	?	?	1	1	0	0	–	0
Tettigonia	?	?	0	0	0	0	–	0	0	?	?	?	?	?	?	?	?	?	?	1	1	0	0	–	0
Locusta	?	?	0	0	0	0	–	0	0	?	?	?	?	?	?	?	?	?	?	1	1	0	0	–	0
Xyela	?	?	0	0	0	0	–	0	0	?	?	?	?	?	?	?	?	?	?	0	0	1	0	–	0
Nevrorthus	?	?	0	0	0	0	–	0	0	?	?	?	?	?	?	?	?	?	?	0	0	1	0	–	0
Zorotypus	?	?	0	0	0	0	–	0	0	?	?	?	?	?	?	?	?	?	?	1	1	0	0	–	0
Trogiomorpha	?	?	0	0	0	0	–	0	0	?	?	?	?	?	?	?	?	?	?	0	1	0	0	–	0
Liposcelis	?	?	0	0	0	0	–	0	0	1	–	0	0	0	0	0	0	0	0	0	1	0	0	–	0
Embidiopsocus	?	?	0	0	0	0	–	0	0	?	?	?	?	?	?	?	?	?	?	0	1	0	0	–	0
Caecilius	?	?	0	0	0	0	–	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	–	0
Trinoton	?	?	–	0	0	0	–	0	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	–	0
Trichodectes	?	?	–	0	0	0	–	0	1	1	0	0	0	1	1	1	0	0	0	0	1	0	0	–	0
Haematomyzus	?	?	–	0	0	?	?	0	1	0	0	0	0	1	1	0	1	1	0	0	1	0	0	0	0
Pediculus	?	?	–	0	0	?	?	0	1	0	0	0	0	1	1	0	1	1	1	0	1	0	0	?	0
Frankliniella	?	?	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	0	1	0	0	0	0
Cacopsylla	?	?	0	0	0	1	0	0	0	?	?	?	?	?	?	?	?	?	?	0	1	0	0	0	1
Aleyrodes	?	?	0	0	0	?	0	0	0	?	?	?	?	?	?	?	?	?	?	0	1	0	0	0	1
Drepanosiphum	?	1	0	0	0	1	0	0	0	?	?	?	?	?	?	?	?	?	?	0	1	0	0	0	0
Pseudococcus	?	?	0	0	0	?	0	0	0	?	?	?	?	?	?	?	?	?	?	0	1	0	0	0	0
Coccus	?	?	0	0	0	?	0	0	0	?	?	?	?	?	?	?	?	?	?	0	1	0	0	0	0
Centrotus	?	1	0	0	0	1	0	0	0	?	?	?	?	?	?	?	?	?	?	0	1	0	0	1	0
Cicadella	?	1	0	0	0	1	0	0	0	?	?	?	?	?	?	?	?	?	?	0	1	0	0	1	0
Cicadetta	?	1	0	0	0	1	0	0	0	?	?	?	?	?	?	?	?	?	?	0	1	0	0	1	0
Cercopis	?	1	0	0	0	1	0	0	0	?	?	?	?	?	?	?	?	?	?	0	1	0	0	1	0
Cixius	?	1	0	0	0	1	0	0	0	?	?	?	?	?	?	?	?	?	?	0	1	0	1	1	0
Javasella	?	1	0	0	0	1	0	0	0	?	?	?	?	?	?	?	?	?	?	0	1	0	1	1	0
Dictyophora	?	1	0	0	0	1	0	0	0	?	?	?	?	?	?	?	?	?	?	0	1	0	1	1	0
Pentatomorpha	1	1	1	1	1	2	1	1	1	?	?	?	?	?	?	?	?	?	?	0	1	0	0	0	0
Systelloderes	0	0	0	1	1	2	1	?	1	?	?	?	?	?	?	?	?	?	?	0	1	0	0	0	0
Ceratocombus	?	0	1	1	1	2	1	?	1	?	?	?	?	?	?	?	?	?	?	0	1	0	0	0	0
Hackeriella	1	1	0	1	0	2	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	0	0	1	0

	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99
Ictinus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	?	0	–	0	0	0	0
Nemoura	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	0	0	1	0
Tettigonia	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	–	0	0	1	0
Locusta	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	–	0	0	1	0
Xyela	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	–	?	0	0	0
Nevrorthus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	0	0	1	0
Zorotypus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	–	0	0	0	0
Trogiomorpha	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0	?	1	0
Liposcelis	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	2	0	0	?	?	1	0
Embidiopsocus	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	2	0	0	?	?	?	0
Caecilius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0	?	1	0
Trinoton	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	1	0	0	2	0	0	0	?	1	0
Trichodectes	0	0	0	0	1	1	1	1	0	0	0	1	1	1	1	1	0	0	2	0	0	0	0	1	0
Haematomyzus	0	0	2	0	1	1	1	1	1	0	1	0	1	1	1	1	0	0	2	0	0	0	0	1	0
Pediculus	0	0	2	0	0	0	0	0	1	1	0	1	1	1	1	1	0	0	2	0	0	0	0	1	0

(*Continued*)

	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99
Frankliniella	0	0	2	0	0	0	0	0	0	2	0	1	1	0	0	0	0	0	2	1	1	0	0	0	0
Cacopsylla	1	1	1	1	0	0	0	0	0	2	0	0	0	0	0	1	0	0	2	1	1	1	0	1	1
Aleyrodes	1	1	1	1	0	0	0	0	0	2	0	0	0	0	0	1	0	0	2	1	1	1	0	1	0
Drepanosiphum	0	0	1	1	0	0	0	0	0	2	0	0	0	0	0	1	0	0	2	1	1	?	0	1	0
Pseudococcus	0	0	1	1	0	0	0	0	0	?	1	1	0	0	1	1	0	0	2	1	1	0	0	1	0
Coccus	0	0	1	1	0	0	0	0	0	?	1	1	0	0	1	1	0	0	2	1	1	0	0	1	0
Centrotus	0	0	2	0	0	0	0	0	0	2	0	0	0	0	0	1	1	1	2	1	1	0	1	1	0
Cicadella	0	0	2	0	0	0	0	0	0	2	0	0	0	0	0	1	1	1	2	1	1	0	1	1	0
Cicadetta	0	0	2	0	0	0	0	0	0	2	0	0	0	0	0	1	1	1	2	1	1	0	1	1	0
Cercopis	0	0	2	0	0	0	0	0	0	2	0	0	0	0	0	1	1	1	2	1	1	0	1	1	0
Cixius	0	0	2	0	0	0	0	0	0	2	0	0	0	0	0	1	1	1	2	1	1	0	0	1	0
Javasella	0	0	2	0	0	0	0	0	0	2	0	0	0	0	0	1	1	1	2	1	1	0	0	1	0
Dictyophora	0	0	2	0	0	0	0	0	0	2	0	0	0	0	0	1	1	1	2	1	1	0	0	1	0
Pentatomorpha	0	0	2	0	0	0	0	0	0	2	0	0	0	0	0	1	0	0	2	1	1	0	0	1	1
Systelloderes	0	0	2	0	0	1	0	0	0	2	0	0	0	0	0	1	0	0	2	1	1	0	?	1	1
Ceratocombus	0	0	2	0	0	0	0	0	0	2	0	0	0	0	0	1	0	0	2	1	1	0	?	1	?
Hackeriella	0	0	2	0	0	0	0	0	0	2	0	1	0	0	0	1	0	0	2	1	1	0	?	1	0

	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117
Ictinus	3	0	–	0	0	1	1	–	–	0	0	0	0	0	0	0	0	0
Nemoura	2	1	0	0	0	1	0	–	–	0	0	0	0	0	0	0	0	0
Tettigonia	3	0	0	0	1	1	0	–	–	0	0	0	0	0	0	0	0	0
Locusta	3	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Xyela	3	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Nevrorthus	3	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Zorotypus	1	0	–	0	0	1	0	–	–	0	0	0	0	0	0	0	0	0
Trogiomorpha	1	0	–	1	0	1	0	–	–	1	0	0	0	0	0	0	0	0
Liposcelis	2	0	–	0	0	1	1	–	–	0	0	0	0	0	0	0	0	0
Embidiopsocus	2	0	–	0	0	1	1	–	–	0	0	0	0	0	0	0	0	0
Caecilius	1	0	–	1	0	1	0	–	–	0	0	0	0	0	0	0	0	0
Trinoton	1	0	–	0	1	1	0	–	–	0	0	0	0	0	0	1	0	0
Trichodectes	0	0	–	0	0	0	0	–	–	0	0	0	0	0	0	0	0	0
Haematomyzus	0	0	–	0	0	3	0	–	–	0	0	0	0	0	0	0	0	0
Pediculus	0	0	–	0	1	0	0	–	–	0	0	1	0	1	0	0	1	0
Frankliniella	1	2	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Cacopsylla	1	3	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Aleyrodes	1	1	0	0	0	1	0	–	–	0	0	0	1	0	0	0	0	0
Drepanosiphum	1	0	–	1	0	1	0	–	–	0	1	0	0	0	0	0	0	0
Pseudococcus	0	0	–	1	0	0	0	–	–	0	0	0	0	0	1	0	0	0
Coccus	0	0	–	1	0	0	0	–	–	0	0	0	0	0	1	0	0	0
Centrotus	2	3	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
Cicadella	2	3	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
Cicadetta	2	0	–	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Cercopis	2	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Cixius	2	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Javasella	2	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Dictyophora	2	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Pentatomorpha	2	0	–	1	0	1	0	–	–	0	0	0	0	0	0	0	0	1
Systelloderes	1	0	–	0	0	1	0	–	–	0	0	0	0	0	0	0	0	1
Ceratocombus	1	0	–	0	0	1	0	–	–	0	0	0	0	0	0	0	0	0
Hackeriella	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 2

Proposed phylogenetically informative characters

The list comprises 118 characters of the head, thorax, abdomen, and attachment structures. They were scored for 25 representatives of Acercaria. As outgroup taxa we chose one representative each of Odonata [*Ictinus angulosus Selys* (Mathur and Mathur, 1961)]; Plecoptera [*Nemouracinerea* (Moulins, 1968)]; Orthoptera [*Locusta migratoria* (Albrecht, 1953) and *Tettigona viridissima* (Henning, 1974)]; Hymenoptera [*Macroxyela ferruginea* (Vilhelmsen, 2000, 2001; Beutel and Vilhelmsen, 2007)]; Neuroptera [*Nevrorthus* sp. (Friedrich and Beutel, 2010)]; and Zoraptera [*Zorotypus hubbardi* (Beutel and Weide, 2005; Friedrich and Beutel, 2008)].

Some characters were taken from the data matrices of other authors:

Main source	Character numbers
Beutel and Gorb (2001)	0–15
Yoshizawa and Johnson (2006)	19–38
Beutel and Gorb (2006)	16–18
Yoshizawa and Johnson (2006)	46, 59–68
Wheeler et al. (1993)	47–55
Beutel et al. (2011)	69–71

0. Rupturing mechanism at the base of the antennal flagellum: (0) absent; (1) present.

A rupture-facilitating cuticle modification is present in Psocodea (Seeger, 1975; Beutel and Gorb, 2001). It is absent in all other examined taxa under consideration.

1. Exposure of mouthparts: (0) largely or completely exposed; (1) left mandible enclosed in a pouch formed by anteclypeal wall, labrum, stipes, and hypopharynx; (2) bases of mandibular and maxillary stylets articulate inside head with mandibular and maxillary plates.

The left mandible is enclosed in a pouch in Thysanoptera (Mickoleit, 1963). The bases of the mandibular and maxillary stylets articulate inside the head with mandibular and maxillary plates in Hemiptera (Carver et al., 1991). The situation is unknown for Rhynchophthirina, Anoplura, and Troctomorpha (coded as ?).

2. Right mandible: (0) present; (1) reduced.

The right mandible is reduced in Thysanoptera (e.g. Mickoleit, 1963).

3. Shape of mandibles: (0) not stylet-like; (1) stylet-like.

Stylet-like mandibles are generally present in Hemiptera (Hamilton, 1981) and have evolved independently within Phthiraptera [Anoplura and Rhynchophthirina (Weber, 1969)]. The left mandible is transformed into a stylet-like structure in Thysanoptera whereas the right mandible is reduced (char. 2). Biting mandibles are present in Psocoptera, *Trimoton* sp. (Amblycera), and *Trichodectes* sp. (Ischnocera).

4. Cardo: (0) present; (1) strongly reduced or absent; (2) fused with stipes.

The cardo is strongly reduced or absent in Hemiptera. This was considered as an autapomorphy of this group by Kristensen et al. (1991). It is completely fused with the stipes in Psocoptera and Phthiraptera and might therefore be an autapomorphy for the Psocodea (Yoshizawa and Saigusa, 2003).

5. Lacinia: (0) absent; (1) present.

The lacinia is missing in Anoplura and Rhynchophthirina (Weber, 1969; Tröster, 1990).

6. Insertion of lacinia: (0) on stipes; (1) detached from stipes.

The lacinia is detached from the stipes in Acercaria (e.g. Rister, 1951; Hamilton, 1981; Kristensen et al., 1991; Beutel and Gorb, 2001; Yoshizawa and Saigusa, 2003). This character is coded as (–) for taxa without lacinae. The lacinia inserts on the stipes in Thysanoptera (Crampton, 1923).

7. Lacinia: (0) not elongate and stylet-like; (1) elongate and stylet-like.

A stylet-like lacinia is present in Acercaria (Badonnel and Grassé, 1951; Carver et al., 1991) and was considered an apomorphy of this group by Kristensen et al. (1991). This character is coded as (–) for taxa without lacinae.

8. Labial rostrum: (0) absent; (1) present.

A labial rostrum is present in Hemiptera (Hamilton, 1981) and was considered an apomorphy of this group by Kristensen et al. (1991).

9. Labial palps: (0) absent or strongly reduced; (1) comprising at least 2 segments.

Labial palps are absent or strongly reduced in Psocoptera (Yoshizawa, 2005), Odonata (Mathur and Mathur, 1961) and Hemiptera (Hamilton, 1981). They comprise two to five segments in Thysanoptera (Priesner, 1968) and four in Xyelidae [Hymenoptera (Beutel and Vilhelmsen, 2007)]. The labial palps of all other examined species bear three segments.

10. Cibarial water-vapour uptake apparatus: (0) absent; (1) present.

The cibarial water-vapour uptake apparatus (Rudolph and Knülle, 1982) was considered an apomorphy of Psocodea (Kristensen et al., 1991). However, it is absent in Rhynchophthirina and Anoplura (Lyal, 1985).

11. Jugal "bar": (0) absent; (1) present.

The presence of a sclerotized jugal bar was considered as a synapomorphy of Acercaria and Holometabola (Hamilton, 1971; Kristensen et al., 1991). The character was coded as (–) for taxa without wings.

12. Abdominal ganglia: (0) more than two separate ganglia; (1) two separate ganglia; (2) one single ganglionic mass.

Two separate abdominal ganglionic complexes are found in Zoraptera (Hennig, 1969). A single ganglionic mass is a possible autapomorphy of Acercaria (e.g. Pendergrast, 1962; Lyal, 1985; Carver et al., 1991; Kristensen et al., 1991).

13. Eyes of immature stages: (0) persist; (1) disintegrate or pulled back proximally into cerebrum.

In Holometabola the compound eyes and ocelli of adults are formed de novo during metamorphosis (e.g. Friedrich and Benzer, 2000). They persist in all examined hemimetabolous species.

14. External wing buds: (0) present; (1) absent.

External wing buds are absent in Holometabola (e.g. Kristensen, 1999; Beutel and Gorb, 2001), except for shallow convexities in secondary larvae of Strepsiptera (Beutel and Pohl, 2006). The character is coded as (–) for wingless taxa.

15. Pupal stage: (0) absent; (2) present.

A pupa generally occurs in Holometabola (e.g. Hymenoptera; (Hinton, 1971) and a similar stage occurs in Thysanoptera (Hennig, 1973). The pupa in Nevrorthidae is aquatic, which is probably an autapomorphy of this group (Aspöck et al., 2012). All other examined species do not have a pupal stage.

16. Appearance of compound eyes: (0) before ultimate immature stage; (1) in ultimate immature stage.

The compound eyes appear before the penultimate life stage in non-holometabolan insects and Strepsiptera (Beutel and Gorb, 2006).

17. Ocelli of immature stages: (0) present; (1) absent.

Ocelli are generally absent in nymphs or larvae of Acercaria and Holometabola. They are also missing in nymphs of some groups of Orthoptera. They are present in Zoraptera, Plecoptera and Odonata (e.g. Beutel and Gorb, 2006).

18. Cerci of immature stages: (0) present; (1) absent.

Cerci are absent in immature stages of Acercaria and Holometabola (Beutel and Gorb, 2006; Yoshizawa and Johnson, 2006), with the possible exception of Strepsiptera (Beutel et al., 2011).

19. Tegulae of the forewing: (0) present; (1) absent.

Tegulae are absent in Heteroptera (Yoshizawa and Saigusa, 2001) and Coleorrhyncha. The character was coded as (–) for wingless groups. The situation is unknown for Coccoidea, Aleyrodidae, and *Embiopsocus* sp. (coded ?).

20. Size and shape of Tegulae: (0) small; (1) enlarged, with broad extension encircling the entire margin.

The tegulae are distinctly enlarged with a broad extension encircling the entire margin in Fulgoromorpha (Yoshizawa and Saigusa, 2001). They are small in Plecoptera, Zoraptera, Trogiomorpha, Psocomorpha, Thysanoptera, Psylloidea, Aphidoidea, and Cicadomorpha. The character was coded as (–) for wingless taxa and groups without tegulae. The situation is unclear for Coccoidea, Aleyrodidae, *Embiopsocus* sp., Odonata, Orthoptera, Neuroptera, and Hymenoptera (coded ?).

21. Attachment of tegulae to body wall: (0) narrow; (1) broad.

The tegulae are broadly attached to the body wall in Thysanoptera (Yoshizawa and Saigusa, 2001) and Xyelidae (Hymenoptera, Hörnschemeyer, 2002). The character was coded as (–) in wingless insects and in those where the tegulae are absent. The situation is unclear for Coccoidea, Aleyrodidae, *Embiopsocus* sp., Odonata, Orthoptera, and Neuroptera.

22. HP and BSc: (0) separated from each other; (1) connected with each other.

The humeral plate (HP) is connected with the basisubcostale (BSc) in Psocoptera, Thysanoptera, Aphidoidea, Psylloidea, Auchenorrhyncha, and Heteroptera (Yoshizawa and Saigusa, 2001). HP and BSc are separated from each other in Plecoptera. The character was coded as (–) in wingless insects. The situation is unknown for the remaining outgroups, Coccoidea, Coleorrhyncha, Dipsocoromorpha, Aleyrodidae, and *Embiopsocus* sp.

23. BSc: (0) distant from 2Ax; (1) closely adjacent with the anteroproximal corner of 2Ax; (2) fused with anteroproximal part of 2Ax.

The basisubcostale (BSc) is in close proximity to the anteroproximal corner of the second axillary sclerite (2Ax) in Psocoptera. The BSc is fused with the second axillary sclerite (Yoshizawa and Saigusa, 2001) in Thysanoptera, Psylloidea, Aphidoidea, Auchenorrhyncha, and Heteroptera. It is distant form the second axillary sclerite in Plecoptera. The character was coded as (–) in wingless insects. The situation is unknown for Coccoidea, Coleorrhyncha, Aleyrodidae, *Embiopsocus* sp., Odonata, Orthoptera, Dipsocoromorpha, Neuroptera, and Hymenoptera.

24. BR and HP + BSc: (0) fused with each other; (1) separated from each other.

The basiradiale (BR) and humerale plate (HP) + basisubcostale (BSc) are separated from each other in Thysanoptera (Yoshizawa and Saigusa, 2001). They are fused in all other taxa under consideration. The character was coded as (–) in wingless insects. The situation is unknown for Coccoidea, Coleorrhyncha, Dipsocoromorpha, Aleyrodidae, *Embiopsocus* sp., Odonata, Orthoptera, Neuroptera, and Hymenoptera.

25. BR and 2Ax: (0) separated from each other; (1) fused.

The basiradiale (BR) and the second axillary sclerite (2Ax) are separated from each other in Thysanoptera and Plecoptera (Yoshizawa and Saigusa, 2001). They are fused in Psocoptera, Psylloidea, Aphidoidea, Auchenorrhyncha and Heteroptera. The character was coded as (–) in wingless insects. The situation is unknown for Coccoidea, Coleorrhyncha, Dipsocoromorpha, Aleyrodidae, *Embiopsocus* sp., Odonata, Orthoptera, Neuroptera, and Hymenoptera.

26. 2Ax: (0) nearly flat; (1) anterior region inflated.

The anterior region of the second axillary sclerite (2Ax) is inflated in Acercaria (Yoshizawa and Saigusa, 2001). It is flat in Plecoptera and Xyelidae (Hymenoptera; Hörnschemeyer, 2002). The character was coded as (–) in wingless insects. The situation is unknown for Coccoidea, Coleorrhyncha, Dipsocoromorpha, Aleyrodidae, *Embiopsocus* sp., Odonata, Orthoptera, and Neuroptera.

27. Anterior axillary folding-line: (0) not forked; (1) forked around distal end of 2Ax, proximal branch running through the distal portion of 2Ax.

The anterior axillary folding-line is forked around the distal end of the second axillary sclerite (2Ax) and its proximal branch is running through the distal portion of the second axillary sclerite in Hemiptera (Yoshizawa and Saigusa, 2001). It is not forked in Plecoptera, Thysanoptera, and Psocoptera. The character was coded as (–) in wingless insects. The situation is unknown for Coccoidea, Coleorrhyncha, Dipsocoromorpha, Aleyrodidae, *Embiopsocus* sp., Odonata, Orthoptera, Neuroptera, and Hymenoptera.

28. Position of PMP: (0) distad 2Ax; (1) posterodistad 2Ax.

The proximal median plate (PMP) is located posterodistad the second axillary sclerite (2Ax) in Acercaria (Yoshizawa and Saigusa, 2001). It is distad 2Ax in Plecoptera. The character was coded as (–) in wingless insects. The situation is unknown for Coccoidea, Coleorrhyncha, Dipsocoromorpha, Aleyrodidae, *Embiopsocus* sp., Odonata, Orthoptera, Neuroptera, and Hymenoptera.

29. PMP: (0) nearly flat; (1) deeply concave.

The proximal median plate (PMP) is deeply concave in Acercaria, whereas it is nearly flat in Plecoptera (Yoshizawa and Saigusa, 2001). The character was coded as (–) in wingless insects. The situation is unknown for Coccoidea, Coleorrhyncha, Dipsocoromorpha, Aleyrodidae, *Embiopsocus* sp., Odonata, Orthoptera, Neuroptera, and Hymenoptera.

30. PMP: (0) almost evenly sclerotized; (1) distal margin sclerotized more strongly than its other regions.

The distal margin of the proximal median plate (PMP) is more strongly sclerotized than its other regions in Psocoptera, Thysanoptera, Sternorrhyncha, and Heteroptera. It is evenly sclerotized in Plecoptera. The character was coded as (?) for Auchenorrhyncha by Yoshizawa and Saigusa (2001) since their PMP is reduced. The character was coded as (–) in wingless insects. The situation is unknown for Coccoidea, Coleorrhyncha, Dipsocoromorpha, Aleyrodidae, *Embiopsocus* sp., Odonata, Orthoptera, Neuroptera, and Hymenoptera.

31. PMP: (0) well sclerotized; (1) reduced, often completely membranous.

The proximal median plate (PMP) is membranous in Auchenorrhyncha whereas it is strongly sclerotized in the other acercarian lineages and in Plecoptera (Yoshizawa and Saigusa, 2001). The character was coded as (–) in wingless insects. The situation is unknown for Coccoidea, Coleorrhyncha, Dipsocoromorpha, Aleyrodidae, *Embiopsocus* sp., Odonata, Orthoptera, Neuroptera, and Hymenoptera.

32. DMP: (0) not divided; (1) divided into 2 sclerites.

The distal median plate (DMP) is divided into 2 sclerites in Acercaria (Yoshizawa and Saigusa, 2001). The character was coded as (?) for Thysanoptera as their DMP is reduced. The DMP is not divided in Plecoptera. The character was coded as (–) in wingless insects. The situation is unknown for Coccoidea, Coleorrhyncha, Dipsocoromorpha, Aleyrodidae, *Embiopsocus* sp., Odonata, Orthoptera, Neuroptera, and Hymenoptera.

33. DMP: (0) distant from 2Ax; (1) placed next to 2Ax, articulating along a convex hinge.

The distal median plate (DMP) is placed next to the second axillary sclerite (2Ax), articulating along a convex hinge in Hemiptera and Thysanoptera. It is distinctly separated from the second axillary sclerite in Psocoptera and Plecoptera (Yoshizawa and Saigusa, 2001). The character was coded as (–) in wingless insects. The situation is unknown for Coccoidea, Coleorrhyncha, Dipsocoromorpha, Aleyrodidae, *Embiopsocus* sp., Odonata, Orthoptera, Neuroptera, and Hymenoptera.

34. DMP: (0) large; (1) reduced in size.

The distal median plate (DMP) is reduced in size in Thysanoptera (Yoshizawa and Saigusa, 2001). The character was coded as (–) in wingless insects. It is large in Plecoptera and the remaining acercarian lineages. The situation is unknown for Coccoidea, Coleorrhyncha, Dipsocoromorpha, Aleyrodidae, *Embiopsocus* sp., Odonata, Orthoptera, Neuroptera, and Hymenoptera.

35. Distal arm of 3Ax and DMP: (0) articulating with each other; (1) not articulating with each other.

The distal arm of the third axillary sclerite (3Ax) does not articulate with the distal median plate (DMP) in Acercaria (Yoshizawa and Saigusa, 2001). They articulate with each other in Plecoptera. The character was coded as (–) in wingless insects. The situation is unknown for Coccoidea, Coleorrhyncha, Dipsocoromorpha, Aleyrodidae, *Embiopsocus* sp., Odonata, Orthoptera, Neuroptera, and Hymenoptera.

36. Anterior arm of 3Ax: (0) present; (1) absent.

The anterior arm of the third axillary sclerite (3Ax) is absent in Thysanoptera and Pentatomomorpha (Yoshizawa and Saigusa, 2001). The character was coded as (–) in wingless insects. It is present in Plecoptera, Psocoptera, Sternorrhyncha, Auchenorrhyncha, Enicocephalomorpha, and Dipsocoromorpha. The situation is unknown for Coccoidea, Coleorrhyncha, Dipsocoromorpha, Aleyrodidae, *Embiopsocus* sp., Odonata, Orthoptera, Neuroptera, and Hymenoptera.

37. 3Ax and BA: (0) separate from posterior margin of forewing base; (1) attached to posterior margin of forewing base.

The third axillary sclerite (3Ax) and the basanale (BA) are situated on the posterior margin of the forewing base in Thysanoptera (Yoshizawa and Saigusa, 2001). The character was coded as (–) in wingless insects. The situation is unknown for Coccoidea, Coleorrhyncha, Dipsocoromorpha, Aleyrodidae, *Embiopsocus* sp., Odonata, Orthoptera, Neuroptera, and Hymenoptera.

38. BA and PMP: (0) separate from each other; (1) fused with each other.

The basanale (BA) and the proximal median plate (PMP) are fused with each other in Psocoptera, Thysanoptera, Psylloidea, Aphidoidea, and Heteroptera. They are separated in Plecoptera. The character was coded as (?) in Auchenorrhyncha due to the reduction of the PMP in this taxon (Yoshizawa and Saigusa, 2001). The character was coded as (–) in wingless insects. The situation is unknown for Coccoidea, Coleorrhyncha, Dipsocoromorpha, Aleyrodidae, *Embiopsocus* sp., Odonata, Orthoptera, Neuroptera, and Hymenoptera.

39. Lateral hypopharyngeal arm (0) present; (1) absent.

The lateral hypopharyngeal arm (loral arm after Matsuda, 1965) is absent in Psocodea (Yoshizawa, 2005) and Zoraptera (Beutel and Weide, 2005). It is present in Thysanoptera, Auchenorrhyncha, Aphidoidea, Psylloidea, Pentatomomorpha, Enicocephalomorpha, Dipsocoromorpha, and Coleorrhyncha (Hamilton, 1981). The situation is unknown for Aleyrodidae, and Coccoidea.

40. Ovarioles: (0) not polytrophic; (1) polytrophic; (2) telotrophic; (3) panoistic.

Panoistic ovarioles are present in Zoraptera and Thysanoptera. Ovarioles of the telotrophic type are present in Hemiptera. Polytrophic ovarioles occur in Psocodea and some groups of Holometabola (Štys and Bilinski, 1990; Kristensen et al., 1991).

41. Maxillary palps: (0) present, with four segments or more; (1) absent or reduced number of segments.

Maxillary palps are absent in Odonata, Hemiptera (Spooner, 1938) and Phthiraptera, with the exception of Amblycera, which have 4-segmented maxillary palps (Marshall, 2003). The number of segments is reduced to three in Thysanoptera. The maxillary palps of all other taxa under consideration comprise four or more segments.

42. Abdominal sternite 1: (0) present; (1) absent.

The abdominal sternite 1 is absent in Acercaria (Kristensen, 1981) with the exception of Thysanoptera. It is also absent in Plecoptera (Illies, 1965).

43. Number of axonemes in spermatozoans: (0) zero; (1) one; (2) two; (3) three.

A biaxonemal flagellum is present in Ischnocera, Anoplura, Troctomorpha, and Trogiomorpha (Dallai and Afzelius, 1991). The flagellum has one axoneme in Zoraptera, Auchenorrhyncha (Kubo-Irie et al., 2003; Dallai et al., 2011; Zhang and Dai, 2012), Pentatomomorpha (Araújo et al., 2011), aphids and psyllids (Bào et al., 1997) and in all outgroups (e.g. Szöllösi, 1975; Quicke et al., 1992; Afzelius and Dallai, 1994). The spermatozoans of Aleyrodidae, and Coccoidea are aflagellate (Bào et al., 1997). The situation is unknown for Coleorrhyncha, Enicocephalomorpha, Amblycera, Rhynchophthirina, Psocomorpha, and Dipsocoromorpha (coded as ?). The flagellum of Thysanoptera has three amalgamated axonemes (e.g. Paccagnini et al., 2006, 2009).

44. Gonangulum: (0) not fused with tergum IX; (1) fused with tergum IX.

The gonangulum is fused with tergum IX in Acercaria and Odonata (Yoshizawa, 2005; Klass et al., 2012). The situation is unknown for Enicocephalomorpha, Dipsocoromorpha, and Phthiraptera.

45. Pretentorium: (0) absent or if present not connecting internal extremities of mandibular lever and corpotentorium; (1) unites internal extremities of mandibular lever and corpotentorium.

The pretentorium connects the internal extremities of the mandibular lever and corpotentorium in adult Fulgoromorpha (Bourgoin, 1986). This is not the case in the other taxa under consideration (see (Albrecht, 1953; Beutel and Vilhelmsen, 2007; Hamilton, 1981; Moritz, 2008). The situation is unknown for Neuroptera, Aleyrodidae, and Coccoidea.

46. Lacinial gland: (0) absent; (1) present.

A lacinial gland is present in Amblycera, Ischnocera, and some members of the Trogiomorpha (coded ? for *Cerobasis* sp.) (Yoshizawa and Johnson, 2006). It is absent in the remaining Psocoptera, Rhynchophthirina (Lyal, 1985), Odonata (Mathur and Mathur, 1961), Orthoptera (Albrecht, 1953), Xyelidae (Hymenoptera) (Beutel and Vilhelmsen, 2007), Zoraptera (Beutel and Weide, 2005), Thysanoptera (Mickoleit, 1963) and Auchenorrhyncha (Butt, 1943), Coleorrhyncha, Heteroptera, and Dipsocoromopha. The situation is unknown for Coccoidea, Aleyrodidae, and Neuroptera.

47. Male genitalia: (0) symmetrical, or if asymmetrical, asymmetry not involving pregenital segments; (1) asymmetrical, this asymmetry often involved pregenital segments.

Asymmetrical genitalia can be found in *Stemmocrypta* sp. (Dipsocoromorpha) (Štys, 1983) and in some Zoraptera (F. Hünefeld, pers. comm). The situation is unknown for Coccoidea and Trogiomorpha. The genitals of all described Ceratocombinae are symmetrical (Štys, 1982).

48. Accessory salivary glands generally: (0) not tubular; (1) of the tubular type.

The accessory salivary glands are generally of the tubular type in Pentatomomorpha (Baptist, 1941; Southwood, 1955; Wheeler et al., 1993). The situation is unknown in Thysanoptera, Psylloidea, Aleyrodidae, and Coccoidea.

49. Number of eye trichobothria of first instars: (0) one or absent; (1) two.

Enicocephalomorpha have less than two eye trichobothria in the first-instar larvae, whereas Pentatomomorpha have two trichobothria (Cobben, 1978; Schuh, 1979; Wheeler et al., 1993). The situation is unknown for all other taxa under consideration.

50. Number of ommatidia in first-instar larvae: (0) 4-5; (1) more than five.

More than five ommatidia are present in the first-instar larva of Coleorrhyncha and Pentatomomorpha, but only four or five in Enicocephalomorpha (Cobben, 1978; Schuh, 1979; Wheeler et al., 1993). The situation is unknown for all other taxa under consideration.

51. Number of tarsomeres in first-instar larvae: (0) one; (1) two.

The tarsi are 2-segmented in the first-instar larvae in Aphidoidea, Auchenorrhyncha, Coleorrhyncha, and Pentatomomorpha. Only one tarsomere is present in Enicocephalomorpha and Dipsocoromorpha (Cobben, 1978; Schuh, 1979; Wheeler et al., 1993). The situation is unknown for the other taxa under consideration.

52. Forewings: (0) completely uniform or if differentiated, not forming a distinct corium-clavus and membrane; (1) forewing divided into a distinct corium-clavus and membrane.

The forewing is divided into a distinct corium-clavus and membrane in all Heteroptera with the exception of Enicocephalomorpha. The character was coded as (–) for wingless taxa (Wheeler et al., 1993).

53. Cephalic trichobothria: (0) absent in adults; (1) present in adults.

Cephalic trichobothria are generally present in adults of Heteroptera (Wheeler et al., 1993) and Coleorrhyncha. They are absent in all other groups under consideration (e.g. Weber, 1969; Hamilton, 1981; Beutel and Weide, 2005; Yoshizawa, 2005).

54. Metathoracic scent gland system: (0) absent; (1) present.

A metathoracic scent gland system is present in Heteroptera (Wheeler et al., 1993; Schuh et al., 2009). It is absent in all other groups under consideration. It was proposed as a synapomorphy of Heteroptera and Coleorrhyncha by Kristensen (1981). However, the examination of a histological cross section series of *Hackeriella veitchi* revealed no metathoracic scent glands.

55. Labium: (0) not tubular; (1) tubular labium with three segments; (2) tubular labium with four segments.

The labium is tube-shaped and 4-segmented in Heteroptera (Stys, 1983) and Coleorrhyncha. It is 3-segmented in the majority of Reduviidae (Weirauch, 2008). A tubular labium with three segments is present in Auchenorrhyncha, Aphidoidea (Matsuda, 1965; Wheeler et al., 1993) and Psylloidea (Weber, 1928). It is not tubular in taxa with biting mouthparts. The situation is unknown for Rhynchophthirina, Anoplura, Aleyrodidae, and Coccoidea.

56. Insertion of tubular labium: (0) posteriorly on the head, (1) anteriorly on the head.

The tubular labium is inserted anteriorly on the head in Heteroptera, whereas it inserts posteriorly on the head in Sternorrhyncha, Auchenorrhyncha, and Coleorrhyncha (Carver et al., 1991; Wheeler et al., 1993; Weirauch and Schuh, 2011). The character was coded as (–) for taxa without a tubular labium. The situation is unknown for Anoplura and Rhynchophthirina (coded ?).

57. Dorsal abdominal glands in immature stages: (0) absent; (1) present.

Dorsal abdominal glands associated with the tergites are usually present in nymphs of Heteroptera (Weirauch, 2006; Weirauch and Schuh, 2011) and probably an autapomorphy for this group. They are absent in all other groups under consideration. However, we did not have nymphs of *Systelloderes* or *Corixidea*, therefore the character was coded as "?" for those groups.

58. Number of antennal flagellomeres: (0) more than 4, (1) 4 or less.

The number of antennal flagellomeres is reduced in Heteroptera and Coleorrhyncha (Weirauch and Schuh, 2011). Only one flagellomere is present in Coleorrhyncha. Two flagellomeres are present in Enicocephalomorpha and Dipsocoromorpha, and three in all examined Pentatomomorpha. The true lice have three or less flagellomeres and Odonata 2–4. All other examined species have multisegmented antennae.

59. Articulations between the mesomere, anterodorsal extension of ventral plate and posterior end of basal plate: (0) absent; (1) present.

In the male genitalia of Troctomorpha, Amblycera, and Ischnocera (Yoshizawa and Johnson, 2006) an articulation is present between the mesomere, the anterodorsal extension of the ventral plate, and the posterior end of the basal plate. It is absent in Psocomorpha, Rhynchophthirina, and Anoplura. The situation in the other taxa under consideration is unclear.

60. Length of basal apodeme of the phallic organ: (0) short; (1) long, longer than basal plate.

The basal apodeme is longer than the basal plate in Amblycera. It is short in Troctomorpha, Psocomorpha, and the remaining true lice (Yoshizawa and Johnson, 2006). The situation is unknown for the other taxa under consideration. It was coded as (–) for taxa without a basal apodeme.

61. Third posterodorsal corner of basal plate: (0) not extended; (1) extended posteriorly.

The third posterodorsal corner of the basal plate is extended posteriorly in Amblycera, whereas it is unmodified in the remaining true lice, in Psocomorpha and in Troctomorpha (Yoshizawa and Johnson, 2006). The situation is unknown for the other taxa under consideration.

62. Basal apodeme of the phallic organ: (0) present; (1) absent.

The basal apodeme is present in Troctomorpha and in Psocomorpha. It is also present in all true lice (Yoshizawa and Johnson, 2006). The situation is unknown for the other taxa under consideration.

63. Width of basal apodeme: (0) narrow; (1) as broad as or broader than basal plate.

The basal apodeme is broad in Ischnocera, Rhynchophthirina, and Anoplura, but narrow in Amblycera, Troctomorpha, and Psocomorpha (Yoshizawa and Johnson, 2006). The situation is unknown for the other taxa under consideration.

64. Ventral plates 1: (0) separated; (1) partly fused anteriorly.

The ventral plates 1 are partly fused anteriorly in Ischnocera, Rhynchophthirina, and Anoplura. They are separated in Amblycera, Troctomorpha, and Psocomorpha (Yoshizawa and Johnson, 2006). The situation in other taxa under consideration is unclear.

65. Ventral plates 2: (0) separated or partly fused; (1) completely fused.

The ventral plates 2 are completely fused in Ischnocera. In the remaining Phthiraptera, Psocomorpha, and Troctomorpha they are separated or only partly fused (Yoshizawa and Johnson, 2006). The situation in other taxa under consideration is unclear.

66. Mesomere of the aedeagus: (0) rounded posteriorly; (1) pointed posteriorly.

The mesomere is pointed posteriorly in Anoplura, Rhynchophthirina, and some Psocomorpha (coded as 1 for *Caecilius* sp.). It is rounded posteriorly in Ischnocera, Amblycera, and Troctomorpha (Yoshizawa and Johnson, 2006). The situation is unknown for the other taxa under consideration.

67. Posteromedian part of basal plate: (0) membranous; (1) sclerotized.

The posteromedian part of the basal plate is sclerotized in Anoplura and Rhynchophthirina. It is membranous in Ischnocera, Amblycera, Psocomorpha, and Troctomorpha (Yoshizawa and Johnson, 2006). The situation is unknown for the other taxa under consideration.

68. Anterior end of mesomere: (0) articulated with basal plate; (1) articulated with paramere.

The anterior end of the mesomere is articulated with the paramere in Anoplura. In the remaining true lice, in Psocomorpha and Trocto-

morpha it is articulated with the basal plate (Yoshizawa and Johnson, 2006). The situation in the other taxa under consideration is unclear.

69. Paired ocelli in nymphs or larvae: (0) absent; (1) present.

Paired larval ocelli are absent in Holometabola (Beutel et al., 2011) and they are also missing in acercarian nymphs. The situation is unknown for nymphs of Coleorrhyncha (coded ?).

70. Intrinsic antennal muscles (Mm. scapopedicellares) in immature stages: (0) absent; (1) present.

The Mm. scapopedicellares are absent in holometabolan larvae (Beutel et al., 2011). The muscle is present in immature stages of all other taxa under consideration. The situation is unknown for nymphs of Coleorrhyncha (coded ?).

71. Ventral metasternal process: (0) absent; (1) present.

The ventral metasternal process is present in Holometabola (Beutel et al., 2011). It is generally absent in the other groups under consideration.

72. Sensory plate organs of pedicel: (0) absent; (1) present.

A sensory plate organ of the pedicel is present in Fulgoromorpha (Bourgoin, 1985). It is absent in all other groups under consideration.

73. Evan's organ: (0) absent, (1) present.

Evan's organ, a sensory pit on the maxillary plate, is present in Auchenorrhyncha and Coleorrhyncha. It is absent in Sternorrhyncha and Heteroptera (Evans, 1973; Bourgoin, 1986). The character was coded as (–) for taxa without a maxillary plate, i.e. those with biting mouthparts. The situation is unknown for Anoplura (coded ?).

74. Ductus ejaculatorius: (0) normal; (1) modified as a sperm pump.

The ductus ejaculatorius is modified as a sperm pump in Psylloidea and Aleyrodidae (Schlee, 1969).

75. Proximal abdomen pediculate by reduction of the 1st and 2nd segment: (0) absent; (1) present.

The proximal abdomen is pronouncedly narrowed by the distinct reduction of the 1st and 2nd segment in Psylloidea and Aleyrodidae (Schlee, 1969). This is not the case in all other examined species.

76. Hind coxae: (0) normally developed; (1) broad, closely adjacent.

The hind coxae are broadened and medially closely adjacent in Psylloidea and Aleyrodidae (Schlee, 1969). This is not the case in all other taxa under consideration.

77. Proboscis: (0) absent; (1) shifted posteriorly between bases of procoxae; (2) not shifted posteriorly between bases of procoxae.

Mouthparts forming a proboscis are present in Hemiptera, Rhynchophthirina, Anoplura, and Thysanoptera. The proboscis is shifted posteriorly and placed between the bases of the procoxae in Sternorrhyncha (Hamilton, 1981).

78. Posterior parts of the head capsule: (0) sclerotized; (1) membraneous.

The posterior parts of the head capsule are membranous in Sternorrhyncha (Hamilton, 1981). This is not the case in all other taxa under consideration.

79. Connective tissue occluding occipital foramen: (0) absent; (1) present.

The foramen occipitale is occluded by connective tissue in Ischnocera, Rhynchophthirina, and Anoplura (Lyal, 1985). This is not the case in all other taxa under consideration.

80. Ovipositor simplified: (0) absent; (1) present.

A simplified ovipositor was proposed as an autapomorphy for Psocodea by Grimaldi and Engel (2005a,b).However, it is normally developed in Psocoptera (Yoshizawa, 2002) and only reduced in Phthiraptera (Boudreaux, 1979; Lyal, 1985). It is also simplified in members of the Enicocephalidae (Wygodzinsky and Schmidt, 1991).

81. Spiracular glands: (0) absent; (1) present.

Spiracular glands are present in Ischnocera, Anoplura, and Rhynchophthirina (Lyal, 1985). They are absent in all other groups under consideration.

82. Extension of the occipital apodeme reaching into the thorax: (0) absent; (1) present.

The occipital apodeme extends into the thorax in Ischnocera, Anoplura, and Rhynchophthirina (Lyal, 1985).

83. Pronotum and procoxae: (0) not fused; (1) fused.

The pronotum is fused with the procoxae in Anoplura and Rhynchophthirina (Piotrowski, 1992). This is not the case in all other groups under consideration.

84. Position of anterior tentorial pits: (0) frontal side of head; (1) absent; (2) shifted dorsally.

The anterior tentorial pits are present in Hemiptera, Thysanoptera, and all outgroups. They are absent in Anoplura and Rhynchophthirina. They are shifted to the dorsal side of the head in Thysanoptera and Hemiptera (Hamilton, 1981). The situation is unknown for Coccoidea and Dipsocoromorpha (coded ?).

85. Fusion of head and thorax: (0) absent; (1) present.

The head is fused with the thorax in Coccoidea (Hamilton, 1981). It is connected with the head by the cervical membrane in all other examined species.

86. Body and head: (0) not flattened; (1) dorsoventrally flattened.

The head and body are distinctly flattened dorsoventrally in Troctomorpha, Phthiraptera, Coccoidea, and Coleorrhyncha.

87. Hind femora: (0) not enlarged; (1) enlarged.

The hind femora are distinctly enlarged in Orthoptera, Troctomorpha, Amblycera, and Ischnocera. Grimaldi and Engel (2005a,b) claimed enlarged hind femora as a synapomorphy of all Phthiraptera, but the hind femora of Pediculidae (Anoplura) and Rhynchophthirina are normally-sized.

88. Meso- and metanotum: (0) not fused; (1) fused.

The meso- and metanotum are fused in Troctomorpha and true lice (Lyal, 1985). They are not fused in all other groups under consideration.

89. Compound eyes: (0) not reduced; (1) only 2 ommatidia or less.

The eyes are reduced in Troctomorpha, Phthiraptera (Lyal, 1985) and Coccoidea. They are more or less well developed in all other groups under consideration.

90. Labial palp: (0) present; (1) absent.

The labial palps are absent in Acercaria (e.g. Hamilton, 1981; Lyal, 1985) with the exception of Thysanoptera.

91. Complex tymbal acoustic system: absent (0); present.

A complex tymbal acoustic system is present in Auchenorrhyncha (e.g. Claridge, 1985). It is absent in all other groups under consideration.

92. Aristate antennal flagellum: (0) absent; (1) present.

An aristate antennal flagellum is present in Auchenorrhyncha and Odonata (Mathur and Mathur, 1961).

93. Malpighian tubules: (0) more than six; (1) six; (2) four or less.

Six Malpighian tubules are present in Zoraptera whereas only four are present in Acercaria (e.g. Wigglesworth and Salpeter, 1962; Kristensen, 1981; Lyal, 1985). Between eight and four are usually present in Holometabola (Beutel et al., 2011)but the number is distinctly higher in *Macroxyela* and other hymenopterans.

94. Labrum: (0) not narrowed; (1) narrowed.

The labrum is distinctly narrowed in Hemiptera and Thysanoptera (Hamilton, 1981).

95. Mandibular and lacinial stylets: (1) unicondylar; (0) dicondylar.

The mandibular and lacinial stylets are unicondylar in Hemiptera and Thysanoptera (Mickoleit, 1963; Hamilton, 1981). The character was coded as (–) for groups without piercing-sucking mouthparts.

96. Pedunculate eggs (with stalk): (0) absent; (1) present.

Pedunculate eggs are produced in Psylloidea and Aleyrodidae (Carver et al., 1991), and similar conditions occur in some species of

Aphidoidea (Quednau and Martin, 2006) and Hymenoptera [Tenthredinidae (Boeve, 1991)]. The eggs are not pedunculate in all other groups under consideration. The situation is unknown for Trocto-morpha (coded ?).

97. Gut with filter chamber containing Malpighian tubules: (0) absent; (1) present.

A filter chamber containing Malpighian tubules is present in the digestive tract of Cicadomorpha (Evans, 1963). This is not the case in the other taxa under consideration (e.g. Albrecht, 1953; Evans, 1963; Rhodes et al., 1997). The situation is unknown for Enicocephalomorpha, Dipsocoromorpha, and Psocoptera.

98. Coronal (= median epicranial) suture: (0) absent; (1) present.

A coronal suture is absent in Hymenoptera (Beutel and Vilhelmsen, 2007), Zoraptera (Beutel and Weide, 2005), Odonata (Mathur and Mathur, 1961) and Thysanoptera. It is present in all other groups under consideration, even though it is only weakly developed in *Liposcelis* sp. (Troctomorpha, Hamilton, 1981).

99. Parempodia on unguitractor plate: (0) absent; (1) elongate and setiform, inserted in an alveolus.

A pair of setiform parempodia inserted in an alveolus is present on the distal part of the unguitractor plate in Pentatomomorpha. In Psylloidea, Enicocephalomorpha, and Dipsocoromorpha the parempodia are present, but the alveolus is not as distinct as in Pentatomomorpha.

100. Number of tarsal segments: (0) one; (1) two; (2) three; (3) more than three.

Only one tarsal segment is present in Ischnocera, Rhynchophthirina, Anoplura, Coccoidea, and Thysanoptera partim [coded as 0/1 (Beutel and Gorb, 2001)]. Two segments are present in *Zorotypus* (Beutel and Weide, 2005), Trogiomorpha, Psocomorpha, Amblycera, Psylloidea, Aleyrodidae, Aphidoidea, and Coleorrhyncha. Three tarsal segments are present in Plecoptera, *Embiopsocus* sp. (Troctomorpha), all investigated Auchenorrhyncha, and Heteroptera. More than three tarsal segments are present in Odonata, *Nevrorthus* sp. and *Xyela* sp. (Hymenoptera).

101. Arolium: (0) absent; (1) present; (2) eversible; (3) bilobed.

A vesicle-like, eversible arolium is in present in Thysanoptera, and is apparently an autapomorphy for this group. A largely unmodified arolium is present in Cercopidae, Cixiidae, Delphacidae, and Fulgoridae, and also in Coleorrhyncha and males of *Corixidea* (Dipsocoromorpha). The arolium is also eversible in Fulgoridae to a certain degree (Frantsevich et al., 2008), but not as strongly as in Thysanoptera. In Membracidae, and Cicadellidae the arolium is distinctly bilobed; the same condition is found in *Psylla* sp. An arolium is absent from *Zorotypus*, Psocodea, Aphidoidea, Coccoidea, Cicadidae, and the remaining Heteroptera.

Beutel and Gorb (2001) claimed that an arolium is present in Miridae (Heteroptera), but this might be due to a misinterpretation. For *Lygus hesperus* (Miridae), for instance, Shrestha et al. (2007)disregards the common nomenclature and refers to the attachment structures as an arolium. However, his figures show clearly that these paired structures are in fact pulvilli.

102. Sticky terminal lip ofarolium: (0) absent; (1) present.

In Fulgoromorpha a sticky terminal lip can be distinguished from the rest of the arolium. This sticky lip is the part of the arolium that actually is in contact with the surface. In Psylloidea the terminal part of the bilobed arolium is also morphologically different from the rest. The character was coded as (–) for taxa without arolium.

103. Pulvilli: (0) absent; (1) present.

Pulvilli are present in Trogiomorpha, Psocomorpha, Coccoidea, and Pentatomomorpha. They are fleshy in *Drepanosiphum* sp., but reduced to thin hair-like structures in other aphids.

In Coccoidea the paired fleshy structures at the inner base of the claws are almost always referred to as claw digitules (Cockerell, 1893; Kondo, 2006). However, it appears very likely that they are in fact pulvilli.

104. Euplantulae: (0) absent, (1) present.

Euplantulae are present on the tarsal segments in Orthoptera, *Xyela* sp. (Hymenoptera),*Trimoton* sp. (Amblycera) and in Anoplura. The euplantulae in *Trimoton* sp. are flat and shovel-shaped, whereas they are pad-like in *Xyela* sp. and Orthoptera.

105. Number of claws: (0) one; (1) two; (2) reduced into spoon-shaped plates; (3) main claw plus accessory claw.

Only one claw is present in Coccoidea and in Pediculidae (Anoplura). In Rhynchophthirina there is a main claw plus a smaller accessory claw. In all other examined species there are two claws. In Thysanoptera the claws are reduced into spoon-shaped, laterally ensheathing plates.

106. Claw teeth: (0) absent; (1) present.

Distinct claw teeth are present in Odonata, *Xyela* sp. (Hymenoptera), Neuroptera, and *Embiopsocus* sp.

107. Protuberance with microtrichia on distolateral side of the pretarsus: (0) absent; (1) present.

A protrusion covered with microtrichia is present on the ventral side of the pretarsus in Cercopidae, on the distolateral region of the arolium, directly below the claws. This condition not found in any other groups is probably an autapomorphy of the family. The character was coded as (–) for taxa without arolii.

108. Sensorial setae on mesal side of arolium: (0) absent; (1) present.

On the distal part of the bilobed arolium of Membracidae and Cicadellidae there are two thin sensillae. Neither on the bilobed arolium of Psylloidea nor on the arolii of the other examined species are such sensilla present.

109. Adhesive claw setae: (0) absent; (1) present.

A thin seta arising from the claws directly distad each pulvillus is present in Trogiomorpha.

110. Eversible structure between tibia and tarsus: (0) absent; (1) present.

An eversible pad between the tibia and tarsus is present in *Macrosiphum* sp. (Aphidoidea). The species with this structure lack fleshy pulvilli (and *vice versa*).

111. Tibial thumb-like process: (0) absent; (1) present.

A tibial thumb-like process (Soler-Cruz and Martin-Mateo, 2009) is present on the ventral side of the apex of the tibia of Pediculidae. A sclerotized spine on the apex of the "thumb" forms a pincer together with the claw.

112. Empodial Paronychium: (0) absent; (1) present.

A thin lobe-like structure arises between the claws in Aleyrodidae. Most authors follow Quaintance and Baker (1913) in referring to this structure as "paronychium". It's still questionable if the structure is homologous with an arolium or an empodium. Further study of the internal fine structure is required.

113. Tarsal apophysis on the ventral side of the tarsus: (0) absent; (1) present.

A spiny tarsal apophysis (= lamella (Keilin and Nuttall, 1930) is present on the ventral side of the tarsus of the head louse and the body louse. This apophysis is placed on a cushion-like structure not mentioned by Soler-Cruz and Martin-Mateo (2009).

114. Two dorsal capitate setae: (0) absent; (1) present.

In Coccoidea two capitate setae [= tarsal digitules after (Cockerell, 1893)] are present on the dorsal side of the pretarsus.

115. Flag-like sensilla on the 1st tarsal segment: (0) absent; (1) present.

Two flag-like sensilla are present on the ventral side of the first tarsal segment of *Trimoton* sp. (Amblycera). Sensilla of this type were not found in any other examined species.

116. Fingerlike process below claw: (0) absent; (1) present.

A fingerlike process beneath the claw is present in *Pediculus humanus capitis*. It has probably a sensory function (proprioreceptor), providing information about the opening angle of the claws (Soler-Cruz and Martín-Mateo, 2009). A very similar structure is present in the body louse (*Pediculus humanis corporis*).

117. Ventral brush: (0) absent; (1) present.

The ventral distal rim of the distal tarsomere of Enicocephalomorpha and Pentatomomorpha bears a row of microtrichia (= ventral brush after Weirauch, 2005). The ventral brush is absent in Dipsocoromorpha and all other taxa under consideration.

Characters not included in the matrix

118. Clasping mechanism with tibia and tarsus of foreleg opposable to apex of femur: (0) absent; (1) present.

The forelegs are uniquely modified as raptorial legs in Enicocephalomorpha (Stys, 1983; Wheeler et al., 1993).

119. Head shape: (0) not conspicuously constricted behind compound eyes, ocelli not located on posterior lobe of head; (1) conspicuously constricted behind compound eyes, ocelli located on posterior lobe.

The head of Enicocephalomorpha is distinctly constricted behind the compound eyes with the ocelli located on a posterior lobe of the head capsule. This is apparently an autapomorphy of the group (Stys, 1983; Wheeler et al., 1993).

120. Forewing-body coupling mechanisms: (0) not developed; (1) coupling mechanisms with push-button system and scutellar frena well developed.

The forewing-body coupling mechanism is present in Pentatomomorpha (Wheeler et al., 1993). The character was coded as (–) for wingless taxa.

121. Adhesive pads on metacoxae: (0) absent; (1) present.

According to Stys (1983) Dipsocoromorpha have adhesive pads on the metacoxae. However, no pads were found in *Ceratocombus australiensis* (Dipsocoromorpha).

3.1.4 Study III

Spangenberg R, Friedemann K, Weirauch C, Beutel RG (2013b). The head morphology of the potentially basal heteropteran lineages Enicocephalomorpha and Dipsocoromorpha (Insecta: Hemiptera: Heteroptera). Arthropod Systematics & Phylogeny 71(2), 103–136.

Abstract: The systematic positions of Enicocephalomorpha and Dipsocoromorpha are still controversial and the available morphological information is very fragmentary. Consequently, head structures of *Cryptostemma* (Dipsocoromorpha: Dipsocoridae) and *Systelloderes* (Enicocephalomorpha: Enicocephalidae) were investigated in detail using SEM, serial sectioning and computer-based 3D-reconstruction. The observed features were compared to putatively homologous structures in Nepomorpha, Leptopodomorpha, Cimicomorpha, and Pentatomomorpha. A cladistic analysis based on 71 cephalic characters scored for 16 heteropteran terminals and outgroup taxa resulted in a strict consensus of two minimum length trees. The monophyly of Heteroptera is strongly supported. However, in the present study, the branching pattern within the group is not compatible with recent hypotheses (e.g., Nepomorpha paraphyletic herein). Characters of the head alone are not sufficient to reconstruct the basal branching events in Heteroptera. This is arguably due to homoplasy related to similar feeding habits. Consequently, we evaluated the cephalic characters based on previously published cladograms. A hypothesis with Enicocephalomorpha as the sister group of the remaining Heteroptera (Euheteroptera), followed by Dipsocoromorpha, required the lowest number of steps. Euheteroptera are supported by the presence of distinct bucculae, and Neoheteroptera (Euheteroptera excl. Dipsocoromorpha) by the presence of paired postoccipital condyles and distinctly bi-lobed principal salivary glands. A conspicuous autapomorphy of Enicocephalomorpha is the distinct constriction of the head capsule posterad of the compound eyes and probably also the elongation of the head and the presence of “scapus sclerites”. Dipsocoromorpha differ strongly form Enicocephalomorpha in their head morphology. Convincing cephalic autapomorphies are lacking. Gerromorpha are characterized by cephalic trichobothria originating in a deep pit and by a quadrangular mandibular lever.

Significance in the present thesis: This study contributes to the controversial phylogeny of Heteroptera. The internal and external morphology of two basal considered taxa Enicocephalomorpha and Dipsocoromorpha is documented for the first time in detail.

Own contribution: 75%

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The head morphology of the potentially basal heteropteran lineages Enicocephalomorpha and Dipsocoromorpha (Insecta: Hemiptera: Heteroptera)

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Abstract

The systematic positions of Enicocephalomorpha and Dipsocoromorpha are still controversial and the available morphological information is very fragmentary. Consequently, head structures of *Cryptostemma* (Dipsocoromorpha: Dipsocoridae) and *Systelloderes* (Enicocephalomorpha: Enicocephalidae) were investigated in detail using SEM, serial sectioning and computer-based 3D-reconstruction. The observed features were compared to putatively homologous structures in Nepomorpha, Leptopodomorpha, Cimicomorpha, and Pentatomomorpha. A cladistic analysis based on 71 cephalic characters scored for 16 heteropteran terminals and outgroup taxa resulted in a strict consensus of two minimum length trees. The monophyly of Heteroptera is strongly supported. However, in the present study, the branching pattern within the group is not compatible with recent hypotheses (e.g., Nepomorpha paraphyletic herein). Characters of the head alone are not sufficient to reconstruct the basal branching events in Heteroptera. This is arguably due to homoplasy related to similar feeding habits. Consequently, we evaluated the cephalic characters based on previously published cladograms. A hypothesis with Enicocephalomorpha as the sister group of the remaining Heteroptera (Euheteroptera), followed by Dipsocoromorpha, required the lowest number of steps. Euheteroptera are supported by the presence of distinct bucculae, and Neoheteroptera (Euheteroptera excl. Dipsocoromorpha) by the presence of paired postoccipital condyles and distinctly bi-lobed principal salivary glands. A conspicuous autapomorphy of Enicocephalomorpha is the distinct constriction of the head capsule posterad of the compound eyes and probably also the elongation of the head and the presence of "scapus sclerites". Dipsocoromorpha differ strongly form Enicocephalomorpha in their head morphology. Convincing cephalic autapomorphies are lacking. Gerromorpha are characterized by cephalic trichobothria originating in a deep pit and by a quadrangular mandibular lever.

Key words

Systelloderes, *Cryptostemma*, *Gerris*, musculature, nervous system, alimentary system, phylogeny, anatomy.

1. Introduction

Heteroptera or True Bugs are a megadiverse group of Hemiptera (>40.000) displaying remarkable morphological variation (e.g., Schuh & Slater 1995; Henry 2009). Despite considerable efforts to reconstruct the phylogeny of the group for more than 30 years (see e.g., Schuh & Weirauch 2011), the higher-level systematics of Heteroptera is clearly an issue of ongoing debate (see e.g., Li et al. 2012b). This controversy concerns in particular the respective positions of Enicocephalomorpha (unique-headed bugs), Dipsocoromorpha (minute litter bugs), Nepomorpha (aquatic bugs), and Gerromorpha (semi-aquatic bugs). The modern era of heteropteran classification

started in the 1950s with attempts to subdivide the polyphyletic Geocorisae, the terrestrial groups, recognized by earlier authors: LESTON et al. (1954) defined Pentatomomorpha (stink bugs and allies) and Cimicomorpha (assassin and plant bugs and relatives), but as other authors during this period they did not apply explicitly phylogenetic (Hennigian) approaches. MIYAMOTO (1961) subsequently suggested a basal position for the unique-headed bugs and the minute litter bugs based on the plesiomorphic condition of the alimentary system. He combined the "Dipsocoridae" and "Enicocephalidae" as "Dipsocorimorpha", a group that was obviously based on symplesiomorphies and that he considered to be "parallel" to Cimicomorpha and Pentatomomorpha. ŠTYS & KERZHNER (1975) created the currently used scheme for the higher-level classification of Heteroptera in which they recognized 7 infraorders: Enicocephalomorpha Stichel, 1955; Dipsocoromorpha Miyamoto, 1961; Gerromorpha Popov, 1971; Nepomorpha Popov, 1968; Leptopodomorpha Popov, 1971; Cimicomorpha Leston, Pendergrast & Southwood, 1954 and Pentatomomorpha Leston, Pendergrast & Southwood, 1954. A phylogenetic evaluation of this scheme was beyond the scope of their publication.

Subsequent attempts to incorporate phylogenetic interpretation into the classification of Heteroptera were made by COBBEN (1968, 1978) in his seminal comparative morphological studies, although he emphasized that cladistic methods were unsuitable to reveal the phylogeny of true bugs due to the high degree of homoplasy within the group (reviewed by SCHUH 1979). COBBEN (1978) proposed Heteroptera to be derived from a "gerromorphan stock", with different groups having evolved to different degrees from this ancestral assemblage. Based on this scheme, he considered Enicocephalomorpha and Dipsocoromorpha to be anagenetically close to the heteropteran ancestor and all other taxa to be more derived.

SCHUH (1979) re-analyzed Cobben's data using explicit cladistic procedures. This analysis placed Enicocephalomorpha as the most basal heteropteran lineage with the complete branching pattern as follows: Enicocephalomorpha + (Dipsocoromorpha + (Gerromorpha + ((Leptopodomorpha + Nepomorpha) + (Cimicomorpha + Pentatomomorpha)))). A study based on 31 morphological characters and 669 base pairs of 18S rDNA (WHEELER et al. 1993) gave further support (at least in some of their analyses) to the phylogeny proposed by SCHUH (1979), and the concept of Enicocephalomorpha, Dipsocoromorpha and Gerromorpha as basal heteropteran lineages was also adopted by SWEET (1979), SCHUH & SLATER (1995), HENRY (2009), CASSIS & SCHUH (2010), and WEIRAUCH & SCHUH (2011) (see also CARVER et al. 1991 [Coleorrhyncha included as most basal branch]). In the cladograms of SCHUH (1979) and WHEELER et al. (1993), Heteroptera are subdivided into the following monophyletic clades: Enicocephalomorpha + Euheteroptera (ŠTYS 1983, 1984) (= Dipsocoromorpha + (Neoheteroptera (= Gerromorpha + (Panheteroptera (= Nepomorpha + (Leptopodomorpha + (Cimicomorpha + Pentatomomorpha))))))). However, the morphology-only analysis of WHEELER et al. (1993) itself does not support Euheteroptera but forms a clade consisting of (Gerromorpha + (Dipsocoromorpha + Enicocephalomorpha)), based on the 1-segmented tarsi in the 1st instar nymphs of these taxa (see corrected version of fig. 3). Apomorphic characters shared among Panheteroptera in the morphological analysis are: the absence of arolia in adults (character #21), the differentiation of the fore wing into corium (leathery part) and membrane (character #22), and the interlocking mechanism linking the hemelytra and the body known as 'Druckknopf' (character #24) (but see WEIRAUCH & CASSIS 2009 for an alternative interpretation on the evolution of this feature).

In two morphological studies focused on male genitalic features it was also attempted to shed light on the relative positions of higher-level heteropteran taxa. A "unique position" was assigned to Enicocephalidae based on an unusual feature of the testes (KUMAR 1964). However, it was pointed out in the same study that testes with a single follicle have likely evolved several times independently within different heteropteran families. Moreover, the interpretations were based on a single character system without a sound phylogenetic concept. Based on characters of the male genitalia YANG (2002) suggested Dipsocoromorpha, Gerromorpha and Nepomorpha together to be monophyletic and placed this assemblage as the sister group to Coleorrhyncha (!) + Enicocephalomorpha + (Leptopodomorpha + Cimicomorpha + Pentatomomorpha). Similar to KUMAR (1964), the phylogenetic approach in this study was problematic and character sampling insufficient.

YOSHIZAWA & SAIGUSA (2001) reported a primitive condition of the forewing base structure of Enicocephalidae likely supporting the basal split of Enicocephalomorpha from the rest of Heteroptera.

Similar to the results of WHEELER et al. (1993), Enicocephalomorpha were placed as the most basal branch in the molecular study of XIE et al. (2008). In contrast, Nepomorpha and Leptopodomorpha were placed as the second and third branches, respectively, with (Gerromorpha + Dipsocoromorpha) and (Pentatomomorpha + Cimicomorpha) as sister groups. A basal position of Enicocephalomorpha is also supported by the analysis of 13 protein-coding genes from mitochondrial genomes (Li et al. 2012a). The drawback of this study is the absence of Dipsocoromorpha in the taxon-sampling and the polyphyly of Cimicomorpha.

The hypotheses proposed by SCHUH (1979) and WHEELER et al. (1993), which place Enicocephalomorpha, Dipsocoromorpha and Gerromorpha as basal lineages, are in conflict with several alternative scenarios. Based on morphological data, MAHNER (1993) tentatively suggested "Cryptocerata" (Nepomorpha) as the sister group to the remaining Heteroptera. However, he explicitly pointed out the uncertain position of Enicocephalomorpha and Dipsocoromorpha in this hypothesis, due to the lack of crucial character data. SHCHERBAKOV & POPOV (2002) analyzed 50 morphological characters and like MAHNER (1993) suggested that Nepomorpha may have to be considered as the first branch within Heteroptera. In the

phylogeny of Shcherbakov & Popov (2002) Enicocephaloidea is placed in the Dipsocoromorpha, which form a clade with Leptopodoidea and Gerromorpha. The most recent and comprehensive multiple gene analysis (18S rDNA, 28S rDNA, 16S rDNA and COI) of Heteroptera was carried out by Li et al. (2012b) using different analytical approaches. Nepomorpha was unambiguously placed as the most basal branch. However, the arrangement of the remaining groups varied very strongly, with Cimicomorpha + Pentatomomorpha being recovered as the only stable sister group relationship among the infraorders (see also Wheeler et al. 1993; Xie et al. 2003; Weirauch & Schuh 2011). Phylogenetic hypotheses on relationships among the heteropteran infraorders except Cimicomorpha and Pentatomomorpha must therefore be considered tentative at best.

Phylogenetic reconstructions for Heteroptera are clearly impeded by sparse and scattered morphological data. Comprehensive data on the internal cephalic morphology of Enicocephalomorpha and Dipsocoromorpha are currently unavailable (e.g. tentorium, musculature, nervous system) and those on members of the Gerromorpha are very limited. The need for more detailed investigations of head morphology, among other morphological character complexes, is underlined by an erroneous placement of Enicocephalomorpha close to Reduviidae (Reuter 1910; Usinger 1932, 1945; China & Miller 1959; Jordan 1972) that was based mostly on superficial similarities of external head structures (Schuh 1986).

Even though the monophyly of Enicocephalomorpha has not been tested in a phylogenetic framework (see e.g., Weirauch & Schuh 2011), the group is likely of single origin judging from the uniquely modified head shape, raptorial legs, and distinctive wing venation. Relationships within the group have not been investigated using phylogenetic procedures. The situation is more critical in Dipsocoromorpha, which have long been suspected to be non-monophyletic (Weirauch & Schuh 2011), although a morphological or combined analysis of the group is lacking as well. However, the first cladistic analysis of Dipsocoromorpha, based on a molecular dataset of 87 Hemiptera including 35 Ceratocombidae, Dipsocoridae, and Schizopteridae, found high support for the monophyly of the entire group and also for the 3 families includes in the analysis (Weirauch & Štys in press).

In addition to the striking lack of anatomical data for both Dipsocoromorpha and Enicocephalomorpha, the biology and ecology of Dipsocoromorpha is poorly known.

Enicocephalomorpha ("Henicocephalidae", Stål, 1860 in Usinger 1932) comprises the two families Enicocephalidae ("Henicocephalinae" in Usinger 1932; 405 species) and Aenictopecheidae ("Aenictopechinae" in Usinger 1932; 20 species) (e.g., Carver et al. 1991; Štys 1995a, 2008; Henry 2009). They are characterized by a bilobed head ("unique-headed bugs") (e.g., Kritsky 1977) and completely membranous wings with a distinct radius, media and cubitus reaching the posterior margin (e.g., Usinger & Wygodzinsky 1960; Jordan 1972; Schuh & Slater 1995). The size of the elongated, often brownish bugs ranges between 2 and 15 mm (Štys 1995a; Banar 2008; Štys & Banar 2008). Micropterous and apterous forms are characterized by the loss of ocelli, reduction of eye size and modification of the pronotum (Wygodzinsky & Schmidt 1991). Enicocephalomorpha are predators of different arthropods or polyphagous (e.g., Wygodzinsky & Schmidt 1991). Some species are likely associated with ants ('myrmecophily') as different life stages were found in ant nests (summarized in Wygodzinsky & Schmidt 1991 and Štys et al. 2010), but do not necessarily feed on their hosts (Schuh & Slater 1995). The area of distribution comprises the southern Nearctic and the Neotropics, the Afrotropical region including Madagascar, the Middle East, the Oriental and Australian regions including New Zealand and the southwestern Pacific (Štys 1995a, 2008).

Dipsocoromorpha comprises the five families Ceratocombidae (52 species), Stemmocryptidae (1 species), Dipsocoridae (51 species), Hypsipterygidae (4 species), and Schizopteridae (229 Species) (Henry 2009). The dipsocoromorph bugs are characterized by their miniaturization and contain some of the smallest heteropterans (0.5–4 mm) (Štys 1995b). The body is much more compact than in Enicocephalomorpha and the appearance of some taxa is similar to that of beetles (Štys 1995e). A characteristic feature, even though not exclusive to the minute litter bugs, is the long setation on the antennal flagellum in many species (except Stemmocryptidae) (Jordan 1972; Štys 1995b). Other head structures are quite variable (e.g., presence or absence of ocelli, number and length of labial segments) (Schuh & Štys 1991; Štys 1995e). Most species are assumed to be predators of small arthropods (Carver et al. 1991; Štys 1995c,d), but members of some genera of Ceratocombidae have been suggested to feed on molds (Štys 1995c). Hypsipterygidae and Stemmocryptidae are restricted to the Oriental regions, but Ceratocombidae, Dipsocoridae, and Schizopteridae have worldwide distributions, typically with highest diversity in tropical areas (e.g., Emsley 1969; Carver et al. 1991; Štys 1995b). Similar to Enicocephalomorpha, their habitats are rather cryptic and include leaf litter and gravel along river banks, and they also occur in nests of ants (Carver et al. 1991). Species of Schizopteridae are in addition collected by screen-sweeping vegetation or canopy fogging (C. Weirauch pers. obs.), indicating that some taxa are vegetation dwelling. Early fossils of Dipsocoromorpha are known from the Triassic/Jurassic boundary (Sherbakov & Popov 2002) and the Lower Cretaceous (Schizopteridae) (Azar & Nel 2010).

In contrast to the former groups, Gerromorpha are very polymorphic and will not be treated here in detail. Instead we refer to Andersen's (1982) comprehensive compilation on this infraorder. Gerromorpha are either elongate and slender (up to 36 mm in Gerridae) or small and stout (ca. 1 mm in Veliidae) (Schuh & Slater 1995). Gerromorph bugs are either polyphagous or predators of other arthropods (Carver et al. 1991; Schuh & Slater 1995). The fossil record of Gerromorpha goes back to the Triassic (Damgaard 2008).

In addition to comprehensive molecular data, morphological studies documenting a broad range of character systems and features are necessary for the reconstruction of a well corroborated phylogeny that allows evolutionary interpretations. This is in particular true for Heteroptera, where current phylogenetic hypotheses are unstable and in clear need of additional character data. The main aim of this study is therefore to provide a detailed documentation of the head morphology (including musculature, tentorium, cephalic nervous system and alimentary tract) for representatives of the potentially basal heteropteran lineages Enicocephalomorpha, Dipsocoromorpha and Gerromorpha. This study will close a major gap in the documentation of head structures across Heteroptera (see e.g., PARSONS 1960a, 1962 for studies on Nepomorpha and Leptopodomorpha). In a second step, characters derived from head structures are phylogenetically explored and analyzed using different approaches, with focus on the basal branching pattern in Heteroptera.

2. Material and methods

2.1. Material

The following specimens were examined:

Cryptostemma waltli Fieber, 1860 (Dipsocoromorpha: Dipsocoridae), Germany: Mindelsee (Lake Constance), in pitfall traps on a fallow, 24.x.1989, leg. Kiechle, det. R. Heckmann (same specimens as in HECKMANN & RIEGER 2001), two specimens.

Gerris sp. (Gerromorpha: Gerridae), Germany: Jena, 11°35′07″E 50°54′23″N, vii.2012, leg. et det. R. Spangenberg, one specimen.

Systelloderes sp. (Enicocephalomorpha: Enicocephalidae), Peru: Cuzco: Wayqecha Research Center, 2821 m, 13°10′22″S 71°35′32″W, 05.xii.2011, leg. et det. C. Weirauch, P11L57 sweep, two specimens (same as in SPANGENBERG et al. 2013).

Cryptostemma waltli was killed in formaldehyde and afterwards stored in 70% ethanol. *Gerris* sp. and *Systelloderes* were fixed and preserved in 70% (*Gerris*) and 95% ethanol (*Systelloderes*). In the following all species listed here will be referred to by the generic name only.

2.2. Scanning electron microscopy

Scanning electron (SEM) micrographs of *Systelloderes* and *Cryptostemma* were taken with a Philips XL 30 ESEM (FEI Company, Oregon, USA) and Scandium 5.0 Software (Soft Imaging System GmbH, Münster, Germany). They were completely dehydrated with ethanol (100%) over several stages. Subsequently, the specimens were dried using HMDS (hexamethyldisilazane) (for details see BROWN 1993) and sputter-coated with gold (EmiTech K500, Quorum Technologies, West Sussex, UK). A rotatable specimen holder was used to mount the sample (see POHL 2010).

2.3. Cross-section series and 3D-reconstruction

One specimen each of *Cryptostemma*, *Gerris* and *Systelloderes* was embedded in Araldite® (Huntsman Advanced Materials, Bergkamen, Germany) for semi-thin cross sectioning (1 µm; *Cryptostemma*, *Systelloderes*) or longitudinal sectioning (1 µm; *Gerris*) with a glass knife on a microtome HM 360 (Microm, Walldorf, Germany). The sections were stained with toluidin-blue. Images of sections for 3D-reconstruction of *Cryptostemma* and *Systelloderes* were taken with a Zeiss Axioplan (Zeiss, Göttingen, Germany), the AnalySIS® documentation system (Soft Imaging System GmbH, Münster, Germany) and a pixelink CCD-camera (PixeLINK, Ottawa, Canada). Figures were processed in Adobe® Photoshop® CS2 Version 9.0 (Adobe Systems Incorporated San Jose, California, USA) and Adobe® Illustrator® CS2 12.0.0 (Adobe Systems Incorporated, San Jose, California, USA). Alignment and three-dimensional reconstructions were done with Mercury Amira® 4.1.2 (Visage Imaging GmbH, Berlin, Germany) and surfaces were smoothed with Autodesk Maya® 7.0 (Autodesk GmbH, Munich, Germany).

2.4. Terminology

The terms dorsal, ventral, anterior and posterior consistently refer to the longitudinal body axis (e.g., vertex dorsal, labium ventral), the mouthparts being considered as extending anteriad from the head capsule (prognathous condition). Muscles are continuously numbered in order of appearance and follow the terminology established in SPANGENBERG et al. (2013). The definition of ridges, sutures and tentorium follows WIPFLER et al. (2011). A suture is interpreted as ecdysial cleavage line whereas a ridge is a cuticular strengthening. In some cases an adaption of this terminology is necessary to facilitate the morphological comparison of different borders throughout the infraorders and with other studies (i.a. "mandibular sulcus", see 3.1. Head).

2.5. Cladistic analysis

The analysis comprises 61 characters of the head of 16 representatives of Heteroptera and two outgroup taxa. Winclada 1.00.08 (NIXON 2002) was used for compiling the matrix and NONA (Ratchet, search settings: 1000 replicates) (GOLOBOFF 1999) and TNT (GOLOBOFF et al. 2008) (Settings Memory: General Ram 200 Mbytes,

Max. trees 99999; Analyze Traditional Search, random seed 999999) for calculating minimum length trees. Only unambiguous character transformations were evaluated. Branch support values (Bremer 1994) were calculated with the "Bremer Support" function implemented in TNT (calculate support with TBR, collapse nodes with support below 0, retain trees suboptimal by 30 steps). Characters were coded as non-additive and of equal weight. For additional character evaluations and character mapping three alternative topologies on earlier hypotheses (Wheeler et al. 1993; Mahner 1993; Shcherbakov & Popov 2002; Li et al. 2012; Xie et al. 2008) were enforced with Winclada ("move branch mode"). The "collapse node mode" was used for collapsing relationships within the infraorders.

3. Results

3.1. *Systelloderes* (Enicocephalomorpha)

The head structures are treated starting with the head capsule, followed by the appendages, the digestive tract including salivary complex, and finally the elements of the cephalic nervous system. The muscles belonging to these structures are treated in the corresponding subsections.

Head capsule

The elongated, prognathous head is very distinctly divided into a cylindrical anterior part, a large globular middle part and a smaller globular occipital region (Fig. 1). The three cephalic portions are separated from each other by constrictions extending across the dorsal and lateral parts of the head. The anterior and middle portions are densely covered with long setae. Minute setae are also present but restricted to the ventro-lateral areas. Pairs of cephalic trichobothria are not recognizable.

The anterior part is formed by the flattened frons (fr), which is located dorsally between the globular compound eyes (ce) (Fig. 1A,B). It is separated from the clypeus by the epistomal ridge (epr) (Fig. 2B). However, the internal strengthening is less distinct. The compound eyes are slightly located ventrad. They are enclosed by a weakly developed circumocular ridge (cor) and bear two setae in the posterior part (Fig. 1B). The ventro-lateral region of the anterior part of the head capsule is formed by the genae (ga). They expand upward in front of the maxillary plates to form a collar, and their anterior margin articulates with the basal margin of the labium (Fig. 1B). Buccula e ("flanges of gena, on each side of basal portion of labium" [Schuh & Slater 1995]) are not developed. The bases of the antennae are located laterally and anterad of the compound eyes. Mandibular and maxillary plates are present on the antero-dorsal side of the anterior head portion between the bases of the antennae. The small triangular and glabrous mandibular plates or lora (lor) originate at the fronto-clypeal border region (cly). Along their posterior margins they are separated from the remainder of the head capsule by the genal suture (gs) (see Andersen 1982). In the stricter sense this is no ecdysial cleavage line (see 2.4.). However, we apply this term for comparison with the detailed study of Andersen (1982). Mesally the lora extend beneath the clypeus along the clypeoloral cleft (clc) (Figs. 1B, 2B). The plates are fused with each other medially beneath the clypeus (Fig. 8D) and with the head capsule on their ventral side caudally. The lora form the dorsal guiding device for the feeding stylets (Figs. 3, 8D). The rectangular, sclerotised maxillary plates (mxpl) bear three long setae on their anterior part and originate anterad the apex of the mandibular plates. They are separated from the latter by the mandibular sulcus (msu) (see Singh 1971; "lorogenal cleft" of Parsons 1968) and from the collar-like part of the genae by the ventral cleft (vc) (Figs. 1B, 2B). The maxillary plates are divided into two bean-shaped subunits which are connected basally. The outer ones enclose the ventrolateral margins of the clypeus (Fig. 8C). The inner subunits are not visible externally (Fig. 3A). They lie below the clypeus and both structures together form the ventral guiding device for the feeding stylets (Fig. 3A). Subgena, subgenal ridges and the frontal and coronal (= epicranial) sutures are not distinguishable.

The middle cephalic subunit is the broadest and highest part of the head capsule and bears a median longitudinal incision. It is mainly formed by the vertex (vx) dorso-laterally (and likely the occiput posteriorly) (Fig. 1A). The paired ocelli (oc) in the postero-dorsal region are separated by the longitudinal incision (Fig. 1A). The ventral closure of the head capsule is not subdivided by any ridges or sutures and tentatively referred to as "gular region" (gu) (Fig. 1B,C).

The postoccipital region (poc) is separated from the middle cephalic region by a weakly developed ridge (pocr) (Fig. 1A). This region of the head capsule is partly retracted into the prothorax (pt) and both structures together form a ball-and-socket joint (Figs. 1B, 3A). The thickness of the lateral sides of the postoccipital region is partly increased (stout paired cuticular condyles, indicated by arrows in Figs. 3 and 9L). The dorsal side is formed by a sclerotised, but thin, lip-like apodeme (Fig. 3A). The diameter of the foramen occipitale is slightly smaller than that of the postoccipital region. The latter merges continuously with the cervix (cv) (Figs. 3A, 9L,M).

Musculature. (M1–M5b). M1 (Figs. 3B, 9M,N): O (= origin) – laterally on the pronotum; I (= insertion) – laterally on the dorsal apodeme of the postocciput; F (= function) – levator and retractor of the head (simultaneous contraction) or rotator. M1a (muscles with a small letter are treated as a separate unit) (Fig. 3B): minute transverse muscle ventrad the anterior region of the dorsal apodeme. M2 (Figs. 3B, 9M,N): O – mesonotum; I – dorsolaterally on the dorsal apodeme; F – levator of the

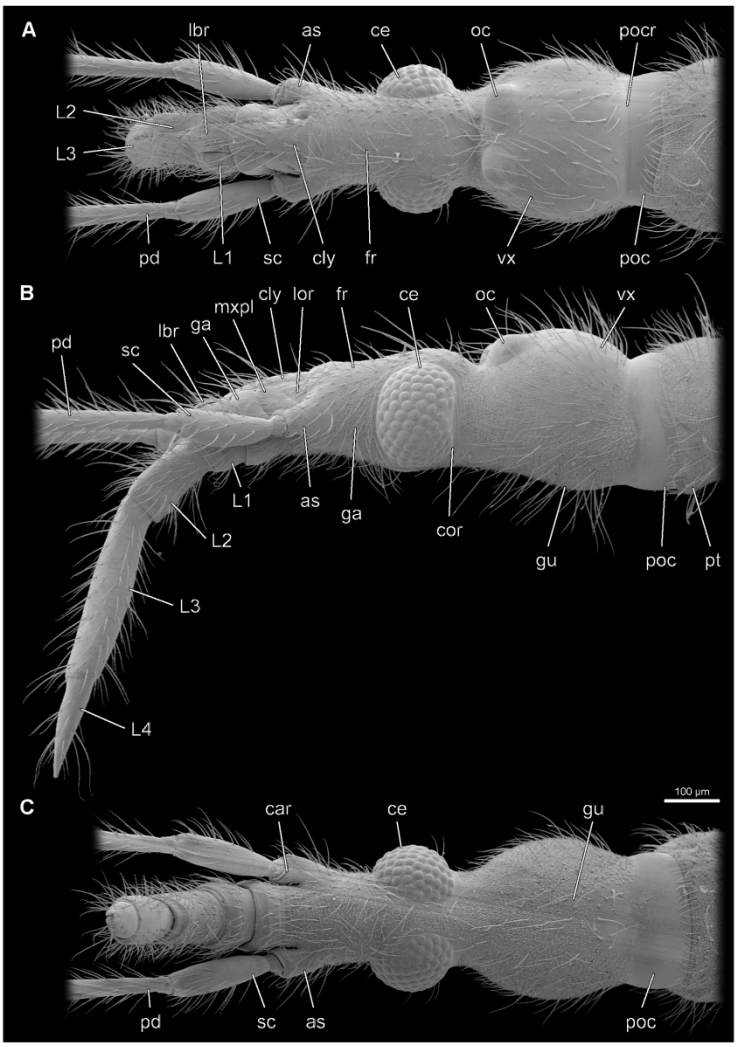

Fig. 1. *Systelloderes* sp.: head and thorax, basi- and distiflagellum omitted, Scanning Electron Micrograph (SEM). **A**: dorsal view; **B**: lateral view; **C**: ventral view. as, antennal socket; car, circumantennal ridge; ce, compound eye; cly, clypeus; cor, circumocular ridge; fr, frons; ga, genal area; gu, gular region; L1–L4, labial segment 1–4; lbr, labrum; lor, lorum/mandibular plate; mxpl, maxillary plate; oc, ocellus; pd, pedicellus; poc, postoccipital region; pocr, postoccipital ridge; pt, prothorax; sc, scapus; vx, vertex.

head. M2a (Figs. 3B, 9M): O – laterally on the pronotum, anterad M1; I – dorsomedially on the dorsal apodeme; F – levator of the head. M3 (Figs. 3A, 9M,N): O – mesal region of the pronotum; I – ventrolaterally on the postocciput; F – depressor of the head. M4 absent. M5 (Figs. 3B, 9M,N): O – anterior side of the profurcal arm; I – ventrolaterally on the cervical membrane, posterad the ventral region of the foramen occipitale; F – depressor and retractor of the head. M5a absent. M5b (Figs. 3B, 9M,N): O – anterior side of the profurcal arm, laterad of M5; I – ventrolaterally on the cervical membrane and laterad M5, posterad the ventral region of the foramen occipitale; F – depressor and retractor of the head.

Tentorium

The tentorium is completely reduced. Anterior and posterior tentorial pits are not developed. Sclerotised elements not belonging to the tentorium but lying within the head cap-

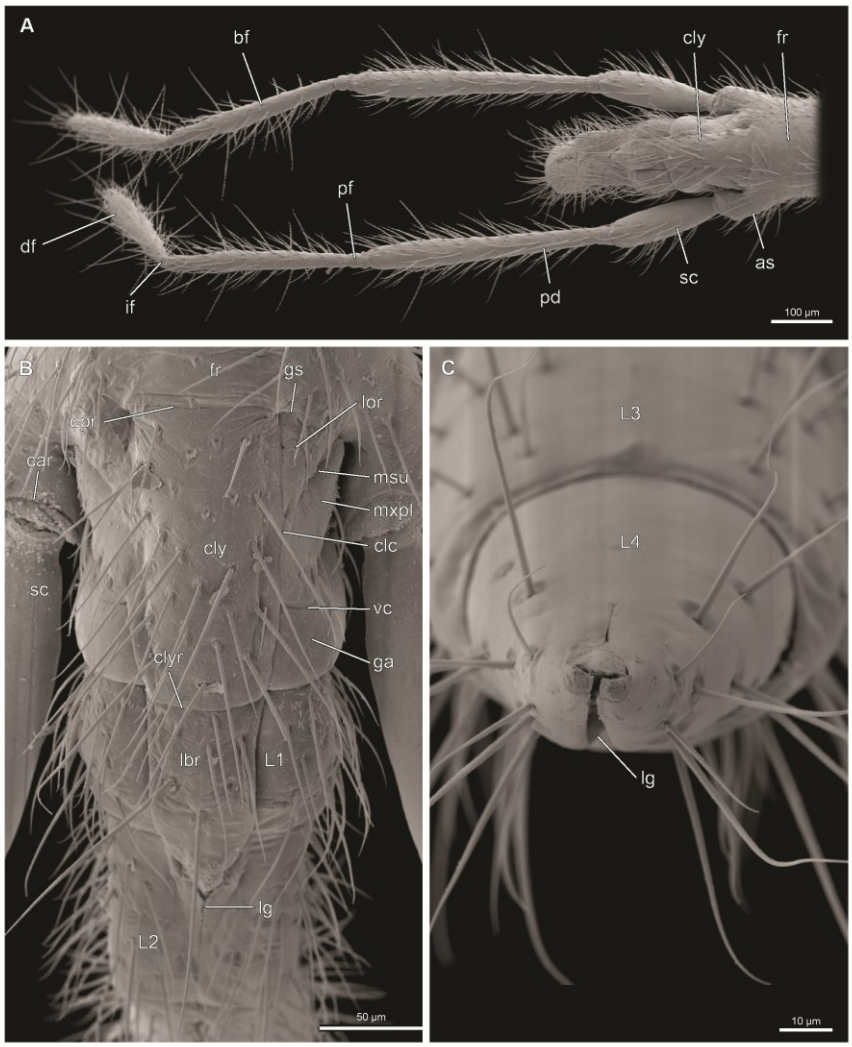

Fig. 2. *Systelloderes* sp.: head, SEM. **A**: dorsal view; **B**: dorsal view, enlarged detail of Fig. 2A; **C**: tip of labium, enlarged detail of Fig. 1C. as, antennal socket; bf, basiflagellum; car, circumantennal ridge; clc, clypeoloral cleft; cly, clypeus; clyr, clypeo-labral ridge; df, distiflagellum; epr, epistomal ridge; fr, frons; ga, genal area; gs, genal suture; if, intraflagelloid; L1–L4, labial segment 1–4; lbr, labrum; lg, labial groove; lor, lorum/mandibular plate; msu, mandibular sulcus; mxpl, maxillary plate; pd, pedicellus; pf, preflagelloid; sc, scapus; vc, ventral cleft.

sule are the hypopharynx, the hypopharyngeal wings, the piston of the salivary pump and the mandibular and maxillary lever, which are treated in the following chapters.

Clypeus and labrum

The rectangular and slightly convex clypeus (cly) is not divided into an anteclypeus, paraclypeus and postclypeus. Its dorsal side is densely covered with long setae (Figs. 1B, 2B). A longitudinal rim functioning as a guiding device for the stylets is present on the ventral side (indicated by an arrow in Fig. 8B). The ventrolateral area of the middle region is interlocked longitudinally with the parts of the gena and of the mandibulary plates that lie beneath the clypeus, for further mechanical support during feeding (Fig. 8D).

The tongue-shaped labrum (lbr) originates along the distal margin of the clypeus (Fig. 1A,B). It is separated from the clypeus by a distinct clypeo-labral ridge (clyr)

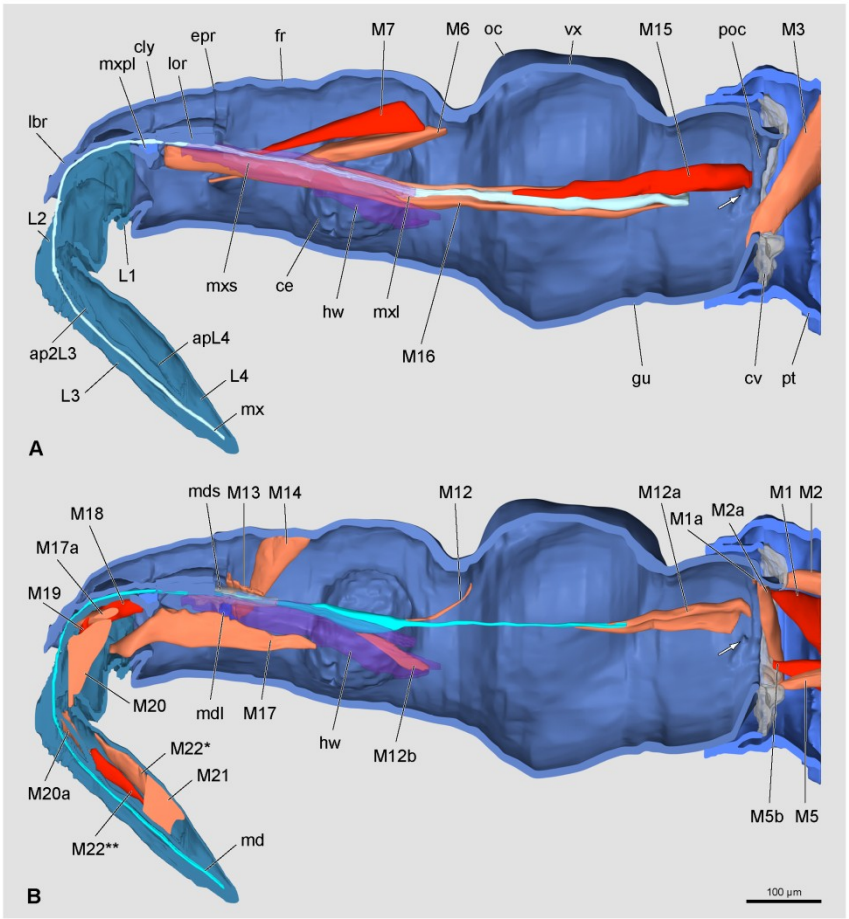

Fig. 3. *Systelloderes* sp.: head and thorax, 3D-reconstruction, sagital section, different muscles and feeding stylets shown (blue: sclerotization, grey: membrane, red: musculature). ap2L3, unpaired bar-shaped apodeme of the 3rd labial segment; apL4, apodeme of 4th labial segment; ce, compound eye; cly, clypeus; cv, cervical membrane; epr, epistomal ridge; fr, frons; gu, gular region; hw, hypopharyngeal wing (semitransparent); L1–L4, labial segment 1–4; lbr, labrum; lor, lorum/mandibular plate; M, muscle with appropriate number (number of muscle corresponds to number in text, Figs. 4–9, Tables 1, 2); md, mandible; mdl, mandibular lever; mds, mandibular sac; mx, maxilla; mxl, maxillary lever; mxpl, maxillary plate; mxs, maxillary sac (semitransparent); oc, ocellus; poc, postoccipital region; pt, prothorax; vx, vertex. Arrow in (B) indicates each partly increased thickness of lateral sides of postoccipal region (see also Fig. 9L).

(Fig. 2B). The dorsal side is densely covered with setae posteriorly while the clypeal longitudinal guiding rim is continued on its ventral side (Fig. 3A). The labrum covers the first labial segment and the base of the second one (Fig. 2B).

Musculature. No muscles are associated with the clypeus and the labrum. M10 and M11 absent.

Antennae

The four-segmented antennae are inserted on a prominent antennal socket (as) anterad the compound eyes and laterad the mandibular and maxillary plates (Figs. 1, 2A). The circumantennal ridge is distinct (car) (Figs. 1C, 2B). An antennifer is absent. The scapus (sc) is cylindrical, densely covered with setae on its lateral side and half as long as the pedicellus (Fig. 2A). The histological section in the plane of the base of the scapus shows two bean-shaped sclerites embedded in the membrane, the "scapus sclerites" (ss) (Figs. 7, 8D). The pedicellus (pd) is more narrow and all sides are covered with setae (Fig. 2A). Its base is connected with membranes to a minute oval sclerite laterally (pp, Fig. 7). This likely

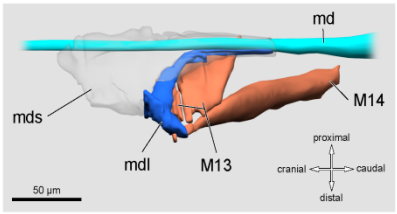

Fig. 4. *Systelloderes* sp.: detail of mandible connected with mandibular lever, 3D-reconstruction (blue: sclerotization, red: musculature). M, muscle with appropriate number (number of muscle corresponds to number in text, Figs. 3, 5–9, Table 1); md, mandible; mdl, mandibular lever; mds, mandibular sac.

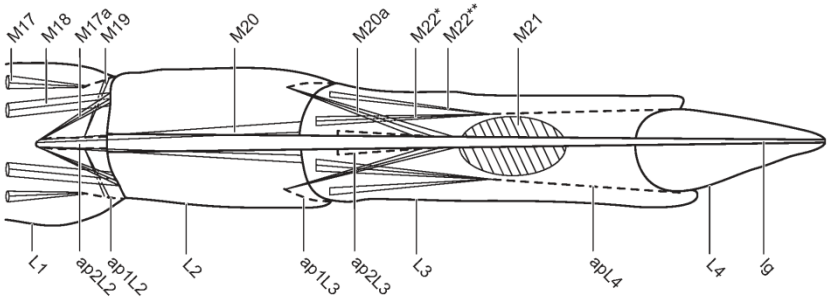

Fig. 5. *Systelloderes* sp.: labium schematic (transparent) and elongated, dorsal view. ap1L2, apodeme of 2nd labial segment; ap2L2; unpaired apodeme of 2nd labial segment; ap1L3, apodeme of 3rd labial segment; ap2L3, unpaired apodeme of 3rd labial segment; apL4, apodeme of 4th labial segment; L1–L4, labial segments 1–4; lg, labial groove; M, muscle with appropriate number (number of muscle corresponds to number in text, Figs. 3, 4, 6–9, Table 1).

represents the "prepedicellite" of Zrzavý (1990). The flagellomere comprises the "basiflagellum" or "basiflagellite" (bf) and "distiflagellum" or "distiflagellite" (df) (see Zrzavý 1990) (Fig. 2A). They are similar in shape, length and setation to the pedicellus. A separate globular and glabrous sclerite is present between the pedicellus and basiflagellum, and between the basiflagellum and distiflagellum, respectively. They likely represent the "preflagelloid Type II" (pf) and "intraflagelloid Type I" (if) of Zrzavý (1990: "hardly sclerotised, thick-walled cylinder with the diameter approximately equal to the height") (Fig. 2A).

Musculature. Extrinsic and intrinsic antennal muscles (M6–M9). M6 (Figs. 3A, 7, 9I): O – roof of the head capsule, border region of the anterior and middle part; I – posterad the ventral base of the scapus; F – depressor of the antenna. M7 (Figs. 3A, 7, 9I): O – roof of the head capsule, anterad O of M6; I – posterad the dorsal base of the scapus; F – levator of the antenna. M8 (Figs. 7, 8B): O – proximal base of the scapus; I – proximal base of the pedicellus; F – extensor of the pedicellus. M9 (Figs. 7, 8B): O – distal base of the scapus; I – distal base of the pedicellus; F – flexor of the pedicellus.

Mandible

The mandibles (md) are a pair of symmetrical, long and slender stylets. Their bases are deeply sunk into the head capsule. Two thirds of their entire length is situated in the head capsule where they reach the posterior margin of the middle cephalic part (Fig. 3B). The proximal halves follow the longitudinal body axis while the distal parts are strongly bent ventrocaudad in resting position (Fig. 3B). The distal parts are crescent-shaped in cross section, with protruding inner edges. They partly enclose the maxillae (Fig. 10). The curved part starts at the level of the first labial segment (L1) (Fig. 3B). The mandibular part located mesad the compound eyes forms a hollow widened tube which opens posterad (Fig. 3B, 8G). The lumen reaches into the apical part (Fig. 10). The proximal opening of the mandibular base is transformed into a long and slender cuticular tendon dorsally (Figs. 3B, 9J).

The mandibles are connected with a curved, acutely triangular, sclerotised mandibular lever (mdl) (type III of Rieger 1976). It is located at a level posterad the antennal socket. The mandibular lever tapers caudally and is transformed into a longitudinal sclerotised stripe anterad the widening (Fig. 4). Only this stripe-part is connected with the mandible directly. The membranous mandibular sac (mds) is attached to the proximal end of the lorum. It partly surrounds the proximal region of the lever and the stylet in the region of the antennal socket (Figs. 3B, 4 and 8E). Mandibular glands are absent.

Musculature. Retractor and promotors of the mandibular stylet (M12–M14). M12 (Fig. 3B): very thin muscle, O – dorsally on the head capsule, on the constriction between the anterior and middle part; I – posterad the widen-

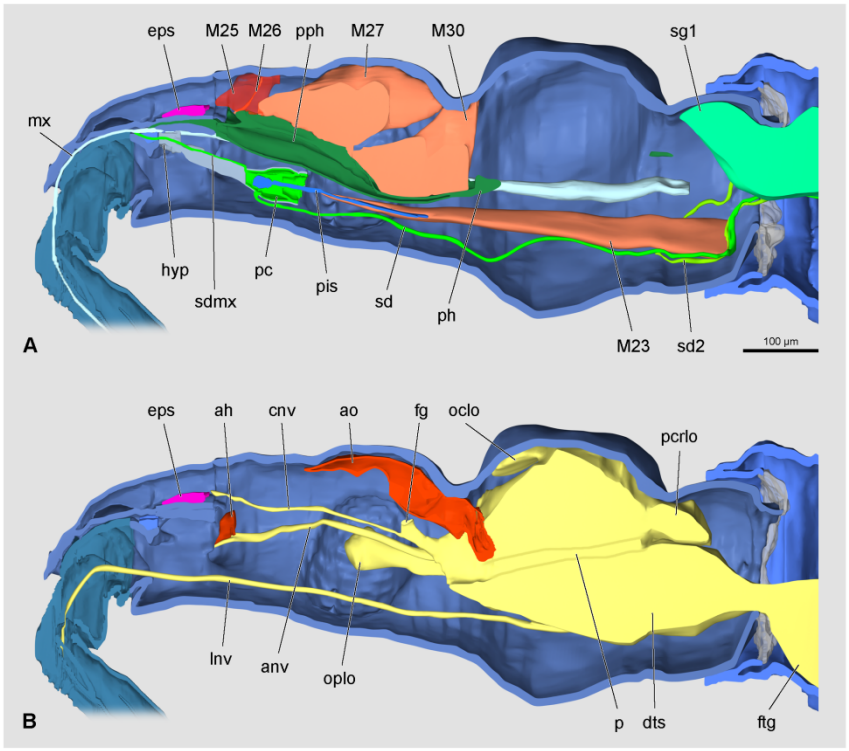

Fig. 6. *Systelloderes* sp.: head and thorax, 3D-reconstruction, sagital section, different muscles, alimentary system (A) and nervous system (B) shown (blue: sclerotization, dark green: pharynx, light green: salivary complex, red: musculature, yellow: nervous system). ah, antennal heart; anv, antennal nerve; ao, aorta cephalica; cnv, clypeo-labral nerve; dts, deuto-tritocerebrum-subesophageal-complex; eps, epipharyngeal sense organ; fg, frontal ganglion; ftg, first thoracal ganglion; hyp, hypopharynx; lnv, labial nerve; M, muscle with appropriate number (number of muscle corresponds to number in text, Figs. 3–5, 7–9, Table 1) (M25 semitransparent); mx, maxilla; oclo, ocellar lobe; oplo, optic lobe; p, passage through brain for aorta and pharynx; pc, pumping chamber; pcrlo, protocerebral lobe; ph, pharynx; pis, piston; pph, prepharynx; sd, common salivary duct; sd2, accessory duct; sdmx, salivary duct connecting pumpnig chamber with salivary channel of maxillae; sg1, principal duct.

ing of the mandible; F – retractor. M12a (Figs. 3B, 9K,L): O – laterally on the distal postoccipital region, dorsad the strengthening of the postoccipital region; I – bar-shaped region of the mandible; F – retractor. M12b (Figs. 3B, 8H, 9I): two small bundles, attached to M16, O – proximal end of the hypopharyngeal wing; I – ventrally on the widened part of the mandible; F – third retractor. M13 (Figs. 3B, 4, 8E): O – dorsally on the border region of head capsule and clypeus; I – laterally on the mandibular lever; F – protractor. M14 (Figs. 3B, 4, 8E): O – dorsally on the roof of the head capsule, anterad the compound eyes; I – laterally on the mandibular lever; F – protractor.

Maxilla

The maxillae consist mainly of the very elongate laciniae. The palp and galea are absent. The proximal elements appear indistinguishably fused, without a recognizable detachment of the lacinia from the stipes. The laciniae, probably together with the parts corresponding with the cardo and stipes (mx), form a pair of hollow, slender stylets. Two thirds of their entire length is situated within the head capsule. Proximally the maxillae reach the anterior region of the posterior cephalic part (Figs. 3A, 9J). The right maxilla originates more proximally than the left one (Fig. 9K). The distal thirds of the stylets (from the beginning of the base of the mandibular plates) are linked with each other forming a dorsal food channel and a ventral salivary channel, with the mesal regions each forming a curved "E" in cross section, with three sclerotised extensions. The food channel (fc) is about twice as large as the salivary channel (sa) and is formed by both stylets to the same extent. In contrast, the ventral extension of the left maxilla is more prominent and thus encloses a larger part of the salivary channel (Fig. 10). The E-shaped structure

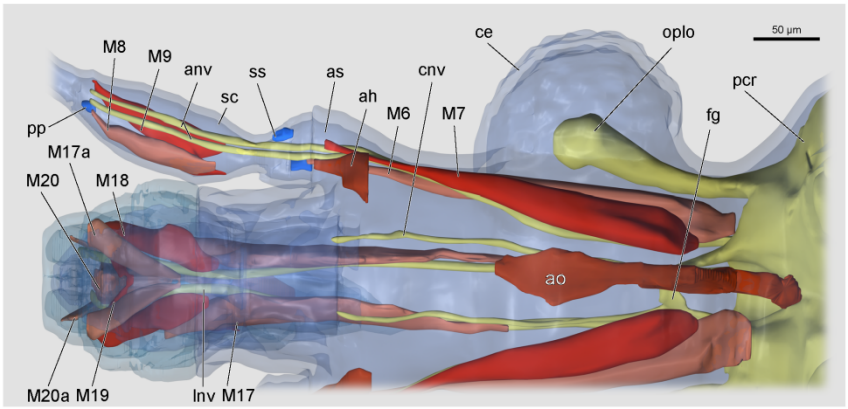

Fig. 7. *Systellodereres* sp.: head (semitransparent), 3D-reconstruction, dorsal view (blue: sclerotization, red: musculature and aorta, yellow: nervous system). ah, antennal heart; anv, antennal nerve; ao, aorta cephalica; as, antennal socket; ce, compound eye; cnv, clypeo-labral nerve; fg, frontal ganglion; lnv, labial nerve; M, muscle with appropriate number (number of muscle corresponds to number in text, Figs. 3–6, 8, 9, Table 1); oplo, optic lobe; pcr, protocerebrum; pp, prepedicellite; sc, scapus; ss, scapus sclerite.

reaches the region posterad the compound eyes (Fig. 9I). The following proximal part of the maxilla is an almost circular widened tube with the opening posterad (Fig. 9J). The membranous maxillary sac (mxs) covers the stylets along the hypopharyngeal wing and maxillary lever (Figs. 3A, 8E). The sac ends proximad the end of the E-shaped region. It is apparently not linked with the head capsule. Maxillary glands are not present.

Musculature. Retractor and promotor of the maxillary stylet (M15, M16). M15 (Figs. 3A, 9J,L): O – laterally on the distal postoccipital region, dorsad the strengthening of the foramen occipitale, ventrad O of M12a; I – dorsally on the maxillary stylet, posterad the E-shaped structue; F – retractor. M16 (Figs. 3A, 9J): one of the largest intrinsic cephalic muscle, O – on the border region of the hypopharynx and maxillary plate; I – ventrolaterally on the proximal circular stylet region; F – promotor.

Labium

The tube-like, four-segmented labium (lab) forms the anterior closure of the head capsule (Fig. 1) and a sheath for the mandibles and the maxillae (Fig. 3). This functional complex is called the "feeding tube" or "suctorial beak". In its resting position its tip is directed ventrally to ventrocaudally (Figs. 1B, 3). The exposed surface of the labium is covered with long setae (Fig. 1B). The proximal[1] sides of segments three and four are glabrous (Fig. 1C). The labial groove (lg) is situated on the distal[1] side of segments two to four (Figs. 2B,C, 5). The four segments are separated from each other by articulation membranes (Fig. 1C). The basal segment (L1) is the shortest (Fig. 1).

[1] The terms distal, proximal, dorsal and ventral refer to the position of the labium as seen in Fig. 1B.

The feeding stylets are placed in a shallow depression on its dorsal side and covered by the clypeus and labrum (Fig. 3.). The second segment (L2) is twice as long as L1. A slender, deep incision on its dorsal side forms transition to the labial groove (Figs. 1B, 2B). Its proximal region is partly retracted into the basal segment. A pair of lateral apodemes originates from its base (ap1L2) and an unpaired bar-shaped apodeme medially from its dorsal edge (ap2L2) (Fig. 5). The third segment (L3) is the longest and twice as long as L2 (Fig. 1B). Its base is partly retracted and bears an apodeme on both sides (ap1L3) (Fig. 5). The floor of the proximal labial groove is strongly sclerotised and forms a bar-shaped apodeme anteriorly (ap2L3) (Figs. 3A, 5). The lateral edges of the groove are interlocked with each other by a groove-and-tongue connection. Two sclerotised extensions ("tongues") on the left side fit with the corresponding folds ("grooves") on the right side (indicated by arrows in Figs. 8B–D). The interlocking mechanism is less tight in the basal and distal region of the segment. The cone-shaped apical labial segment (L4) is about as long as L2 (Fig. 1B). Two bar-shaped apodemes (apL4) originate on its base and reach into L3 over half its length (Figs. 3A, 5). Three furrows are present at the apex. A row of sensilla is not recognizable (Fig. 2C). Intercalary sclerites are not present in the labium.

Musculature. Extrinsic and intrinsic labial muscles (M17–M22). M17 (Figs. 3B, 5, 7, 8G): largest extrinsic labial muscle, O – ventrally on the anterior half of the hypopharyngeal wing; I – ventrally on the base of L2; F – extensor of the labium. M17a (Figs. 3B, 5, 7, 8B): O – laterally on the proximal part of the unpaired apodeme ap2L2; I – distal region of L1, dorsad the paired apodeme ap1L2; F – flexor of the labium (simultaneous contraction) or rotator. M18 (Figs. 3B, 5, 7, 8B): O – dorsally on the roof of the anterior part of the head capsule; I – near

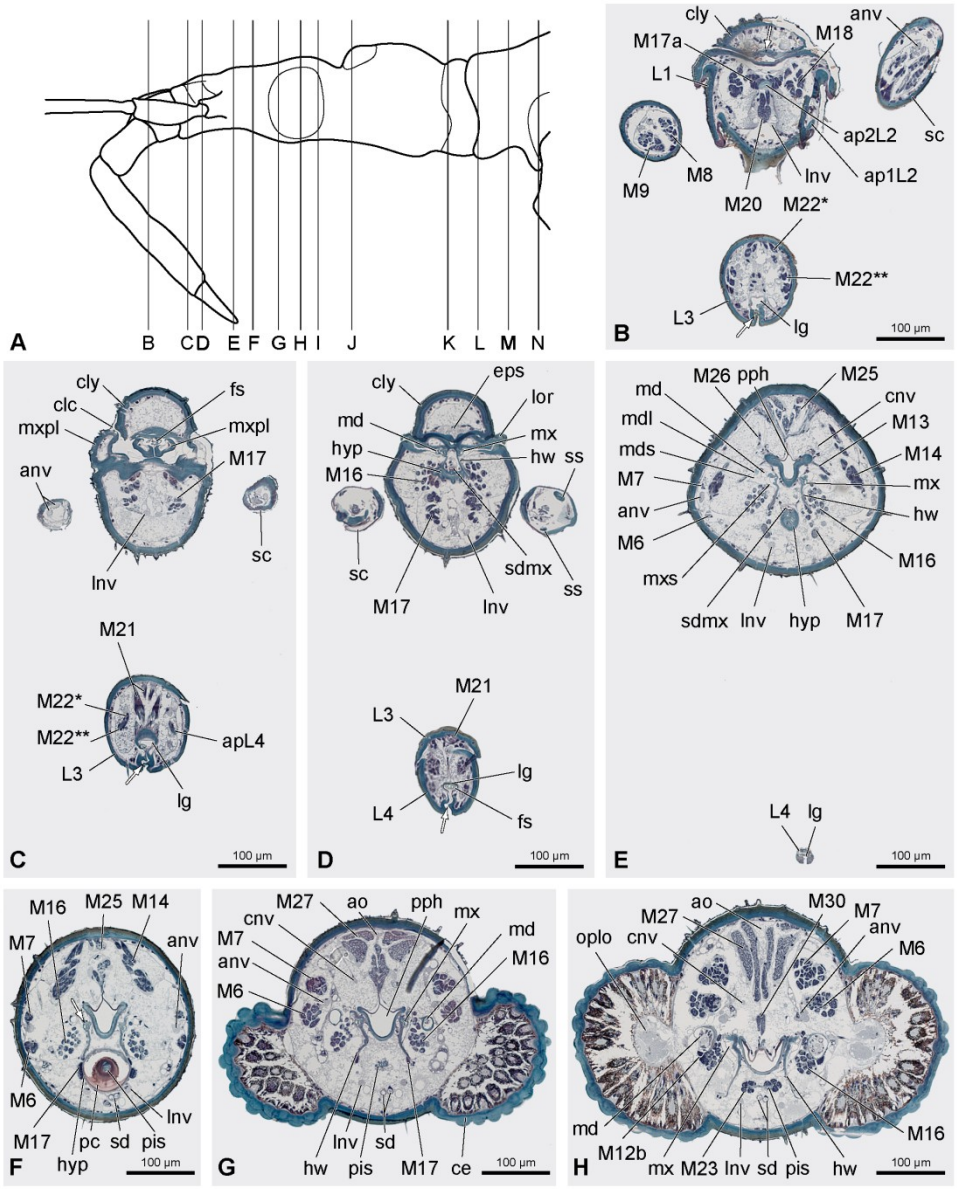

Fig. 8. *Systelloderes* sp.: head and thorax, cross sections. **A**: head and thorax, schematic, lateral view showing planes of section of light micrographs **B**–**N** (continued in Fig. 9). anv, antennal nerve; ao, aorta cephalica; apL4, apodeme of 4th labial segment; ce, compound eye; clc, clypeoloral cleft; cly, clypeus; cnv, clypeo-labral nerve; eps, epipharyngeal sense organ; fg, frontal ganglion; fs, feeding stylets; hw, hypopharyngeal wing; hyp, hypopharynx; L1–L4, labial segment 1–4; lg, labial groove; lnv, labial nerve; lor, lorum/mandibular plate; M, muscle with appropriate number (number of muscle corresponds to number in text, Figs. 3–7, 9, Table 1); md, mandible; mdl, mandibular lever; mds, mandibular sac; mx, maxilla; mxpl, maxillary plate; mxs, maxillary sac; oplo, optic lobe; pc, pumping chamber; pis, piston; pph, prepharynx; sc, scapus; sd, common salivary duct, sdmx; salivary duct connecting pumpnig chamber with salivary channel of maxillae; ss, scapus sclerite. Upper arrow in (B) indicates longitudinal rim functioning as a guiding device for the stylets (the latter are damaged in this slice); lower arrow in (B–D) indicates interlocking of lateral edges of labial groove. Arrow in (F) indicates linkage of maxillae and hypopharyngeal wing (see also Fig. 8E,G).

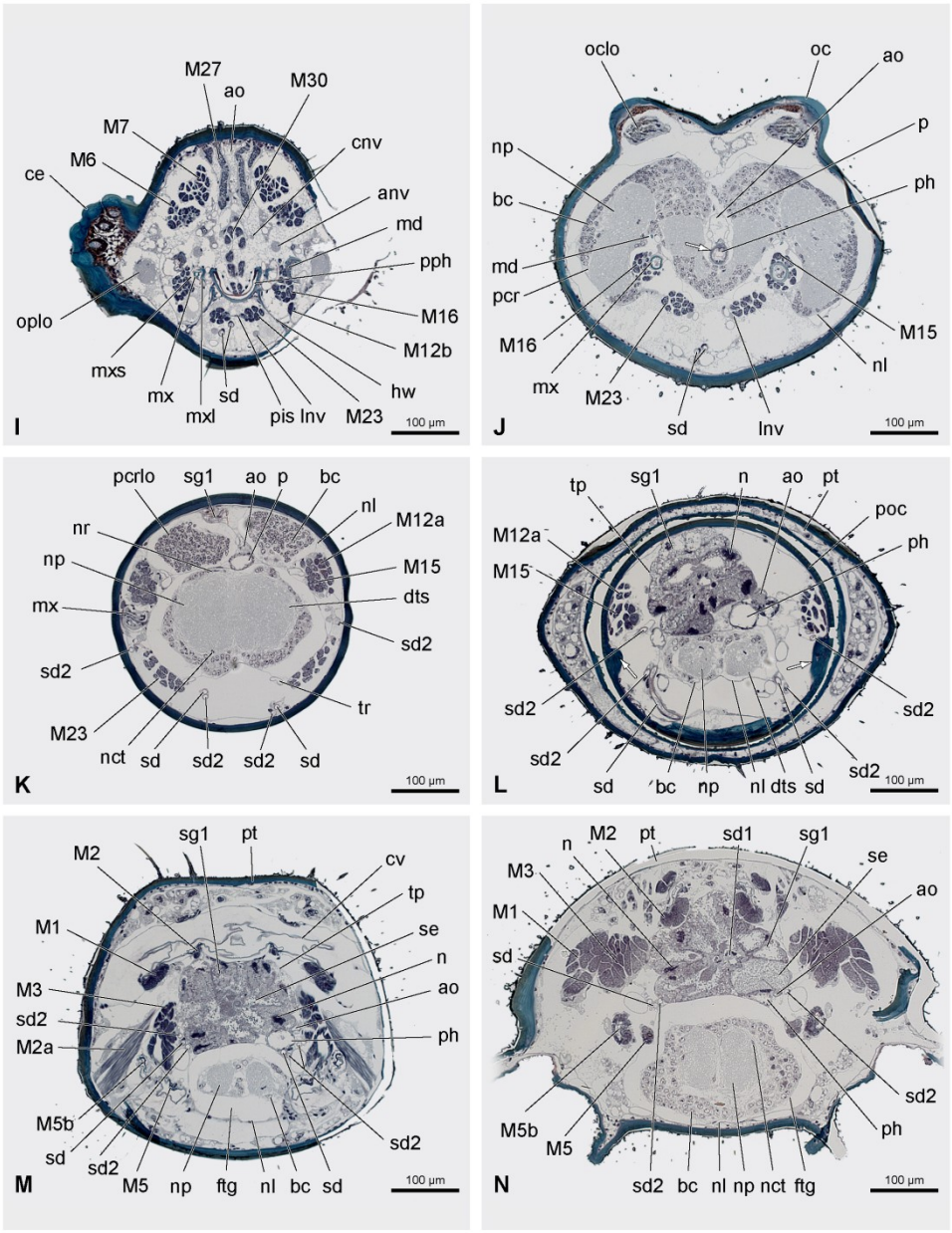

Fig. 9. *Systelloderes* sp.: head and thorax, cross sections, Fig. 8 continued. anv, antennal nerve; ao, aorta cephalica; bc, bark cell; ce, compound eye; cnv, cylpeo-labral nerve; dts, deuto-tritocerebrum-subesophageal-complex; ftg, first thoracal ganglion; hw, hypopharyngeal wing; lnv, labial nerve; M, muscle with appropriate number (number of muscle corresponds to number in text, Figs. 3–8, Table 1); md, mandible; mx, maxilla; mxl, maxillary lever; mxs, maxillary sac; n, nucleus; nct, nucleus of connective tissue; nl, neural lamella; np, neuropil; nr, neurilemma; oc, ocellus; oclo, ocellar lobe; oplo, optic lobe; p, passage through the brain for pharynx and aorta; pcr, protocerebrum; ph, pharynx; pis, piston; poc; postoccipital region; pph, prepharynx; pt, prothorax; sd, common salivary duct; sd1, principal duct; sd2, accessory duct; se, secretion granules; sg1, principal gland; tp, tunica propria; tr, trachea. Arrow in (J) indicates ring muscle layer. Arrow in (L) indicates each partly increased thickness of lateral sides of postoccipal region (see also Fig. 3).

the paired apodeme ap1L2, ventrad I of M17; F – flexor of the labium (simultaneous contraction) or rotator. M19 (Figs. 3B, 5, 7): smallest labial muscle, O – laterally on the unpaired apodeme ap2L2; I – paired apodeme ap1L2, ventrad I of M18; F – support of M17 and M18. M20 (Figs. 3B, 5, 7, 8B): largest intrinsic labial muscle, unpaired, O – ventrally on the unpaired apodeme ap2L2 and dorsally on L2; I – dorsally on L3 and its paired apodemes; F – flexion of L3 and L4. M20a (Figs. 3B, 5, 7): O – laterally on the apodemes ap1L3; I – strengthening of the floor of the labial groove in L3; F – pulls the floor of the labial groove upwards, closes the lateral sides of the labial groove (locking mechanism of the feeding stylets). M21 (Figs. 3B, 5, 8C): unpaired, stout muscle, O – dorsal region of L3, posterior part; I – floor of the labial groove in L3; F – pulls the floor of the labial groove upwards and closes the lateral sides of the labial groove (locking mechanism of the feeding stylets) and likely extension of L4 (connection over the labial floor). M22* (Figs. 3B, 5, 8B): first partition of M22, O – dorsal region of L3, anterior part; I – dorsally on the apodemes apL4; F – flexion (simultaneous contraction) or rotator of L4. M22** (Figs. 3B, 5, 8B): second partition of M22, O – laterally on the anterior side of L3; I – ventrally on the apodemes apL4; F – flexion (simultaneous contraction) or rotator of L4.

Hypopharynx, salivary pump and salivary glands

The sclerotised hypopharynx (hyp) is composed of a slender flattened anterior part ("hypopharyngeal lobe" of CRANSTON & SPRAGUE 1961) and a widened area posterad. The anterior part is fused with the head capsule at a level of the base of the maxillary plates, and is partly connected by membranes with the base of the mesal region of the mandibular plate (Figs. 6A, 8D). In this area it forms two protrusions dorsally which enclose the efferent salivary duct (sdmx, see below) (Fig. 8D). The posterior third of the hypopharynx is almost globular and widens to a bowl-shaped structure enclosing the membranous pumping chamber (Figs. 6A, 8E,F).

The plate-like hypopharyngeal wing (hw) arises at the anterior fifth of the hypopharynx and extends along the E-shaped mesal edge of the maxillary stylet (Fig. 3A). Its posterior region is fused with the short and flattened maxillary lever (mxl) (Figs. 3A, 9I). The two upper extensions of the stylet each fit into a corresponding fold of the wing and lever, while the third ventral one encloses a protrusion (Figs. 8E–G, indicated by an arrow). Posterior to the compound eyes its proximal part forms a membranous connection to the ventral region of the head capsule (Fig. 9I). The wing and lever provide a guiding device for the maxillary stylet.

The functional complex of the salivary pump comprises the bowl-like part of the hypopharynx, the pumping chamber, the piston, the salivary glands, the salivary ducts and the retractor muscle of the piston. The membranous pumping chamber (pc) is anterodorsally linked with the efferent salivary duct (sdmx), which forms the connection with the salivary channel of the maxillae (Figs. 6A, 8E). The duct lies above the hypopharynx and enters the salivary channel in the region of the base of the mandibular plate (Fig. 6A). The paired long and slender common afferent salivary ducts (sd) are fused anterad, just before they enter the pumping chamber anteroventrally (Figs. 6A, 8F). The common salivary duct originates in the cervical region where the principal and accessory duct fuse, enclosed by the principal gland (Fig. 8M,N). The principal duct (sd1) is very short (Fig. 8N) while the accessory duct (sd2) is long and slender and forms a loop in the middle part of the head capsule (Figs. 6A, 9K,M). The sac-shaped principal gland (sg1) is composed of few large cells with a circular arrangement (Figs. 6A, 9L). The cells are densely filled with secretion granules (se) enclosing a bean-shaped nucleus (n) (Fig. 9L,M). The thin tunica propria (tp) forms the external tissue layer (Fig. 9M). Innervations are not recognizable. Detailed information on the accessory gland is given in MIYAMOTO (1976) and COBBEN (1978).

The sclerotised piston (pis) is connected membranously with the pumping chamber (Figs. 6A, 8F). It is composed of a short ovoid anterior part and a long flattened posterior part with a bifurcated ending (Figs. 6A, 9I). The transition region to the ovoid part is strongly folded in cross section (Fig. 8G).

Musculature. M23 (Figs. 6A, 8H, 9K): one of the largest muscles of the head, O – lateroventrally on the postoccipital region, ventrad the strengthened part; I – laterally on the middle region of the piston, enclosing of the bifurcated ending; F – contraction results in an extension of the pumping chamber and influx of saliva from the salivary glands; relaxation pulls the piston back into the pumping chamber which pumps saliva through the salivary duct (sdmx) to the maxillary salivary channel. M24 absent.

Epipharynx

The epipharynx is not present as a clearly defined structure. It may be represented by a flat area of the caudal clypeal region. The density of the tissue in the caudoventral clypeal region is distinctly higher than in the surrounding medium. It is likely that this flattened agglomeration of cells is the epipharyngeal sense organ (eps) (Figs. 6, 8D). Some authors (e.g. CRANSTON & SPRAGUE 1961) also assigned the dorsal region of the food pump to the epipharynx.

Musculature. No musculature is associated directly with the epipharynx.

Pharynx

The pharynx is divided into two regions which are distinctly different anatomically and histologically. The precerebral part ("food pump") has a wide lumen and reaches from the origin of the maxillary food channel to

the anterior part of the brain (prepharynx, pph) (Fig. 6A). It is followed by a "intracerebral" part with a distinctly narrowed lumen (pharynx *sensu stricto*, ph) (Fig. 9J). In cross section the precerebral pharynx appears U- to V-shaped. Ventrolaterally it is strongly sclerotised whereas the dorsal part forms a membranous cover which is prolonged as a tendon dorsally (Fig. 8E–G). The tendon is the attachment side for the anterior cibarial muscle bundles (Fig. 6A). In the posterior region the muscle inserts directly on the dorsal side of the pharynx (Fig. 9I). The transition to the tube-like "intrarcerebral" part is abrupt (Fig. 6A) and marked by the presence of a ring muscle layer (indicated by an arrow in Fig. 9J), which is less strongly developed in the posterior part.

Musculature. Pharyngeal muscles (M25–M30). Longitudinal muscles not recognizable. M25 (Figs. 6A, 8E): unpaired, V-shaped, O – dorsally on the roof of the head capsule, posterad the epistomal ridge; I – dorsally on the tendon of the precerebral pharynx; F – dilation of the cibarium. M26 (Figs. 6A, 8E): a paired delicate muscle, O – dorsally on the roof of the head capsule, posterad the epistomal ridge, laterad the O of M25; I – laterally on the anterior region of the precerebral pharynx; F – dilator. M27 (Figs. 6A, 8H, 9I): unpaired, V-shaped, O – dorsally on the roof of the head capsule, mesad the compound eyes, posterad the O of M25; I – with a tendon on the precerebral pharynx, posterad the I of M26; F – dilator. M28 absent. M29 absent. M30 (Figs. 6A, 8H, 9I): unpaired, O – dorsally on the incision between the anterior and middle part of the head capsule; I – dorsally on the posterior part of the prepharynx; F – dilator.

Brain

The brain is largely restricted to the middle part of the head capsule and nearly fills out its entire lumen (Fig. 6B). The cephalic part of the central nervous system is subdivided into the protocerebrum (pcr) and a compact complex comprising the deuto- and tritocerebrum and the subesophageal complex (dts). The protocerebrum is composed of two connected lateral lobes which cover the proximal region of the brain, and two short lobes (pcrlo) at the posterior end. The latter are directed caudad and reach the postoccipital region (Figs. 6B, 7, 9J). The lateral lobes provide a narrow passage (p) for the pharynx and aorta cephalica (Figs. 6B, 9J). The circumesophageal connectives are very broad, short and compact, and hardly recognizable as separate structures. The optic lobes (oplo) originate on the anterior region of the lateral protocerebral lobes (Figs. 7, 9I). A short nerve tract connects the ocellar lobes (oclo) to the dorsal side of the lateral lobes (Figs. 6B, 9J). The elongated unit formed by the deuto- and tritocerebrum and the subesophageal complex (dts) is distinctly separated from the first prothoracal ganglion (ftg) by two short, mesally fused connectives (Figs. 6B, 9L–N). The paired labial nerves (lnv) originate ventrally in the middle region of the subesophageal complex (Figs. 6B, 8C, 9J). The paired antennal nerves (anv) arise

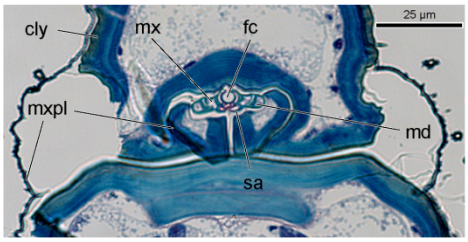

Fig. 10. *Systelloderes* sp.: head, cross section, plane of section anterad Fig. 8C. cly, clypeus; fc, food channel; md, mandible; mx, maxilla; mxpl, maxillary plate; sa, salivary channel.

anteriorly from the deutocerebral region mesad the optic lobes (Figs. 6B, 9I). In the same area the short frontal connectives originate which connect the protocerberal region with the arched frontal ganglion (fg) (Figs. 6B, 7). Two long nerves (cnv), extending into the clypeal region originate on the anterior part of the frontal ganglion. They end close to the assumed epipharyngeal sense organ (Figs. 6B, 7, 8H). The hypocerebralganglion is not distinguishable. Maxillary and mandibular nerves could not be reconstructed precisely with the available section series.

A thin neural lamella (nl) forms the external cell layer of the brain, followed by a sparsely developed neurilemma (nr) composed of few flattened cells. A bark cell layer (bc) (Graichen 1936) of variable thickness encloses the dense internal neuropil (np). The bark cell layer is distinct in the anterolateral region of the protocerebrum and the caudal lobes, reduced to a thin layer in the deutotritocerebrum-subesophageal-complex, strongly reduced in the circumesophageal connectives, and absent in the labial, antennal and clypeolabral nerves. The neuropil is less dense in the connectives and contains scattered single nuclei of the connective tissue (nct) (Fig. 9J–N).

Aorta cephalica and antennal hearts

The aorta (ao) is attached to the pharynx dorsally (Figs. 6, 9J). Anterad the middle part of the head capsule the lumen of the aorta widens (Fig. 7). It is shifted dorsad and situated between the bundles of the V-shaped cibarial dilators. The antennal hearts (ah) are placed in the dorsal region of the antennal socket (Fig. 7). The transition to the aorta cephalica could not be reconstructed precisely with the available section series.

3.2. *Cryptostemma waltli* (Dipsocoromorpha)

Like in the previous morphological section the head structures are treated in a morphology-based sequence. In some cases only differences to *Systelloderes* are pointed out.

Head capsule

The ellipsoid head capsule is prognathous. It is partly retracted into the prothorax (Figs. 11, 14). The dorsal and lateral areas bear a sparse vestiture of long and short setae (Fig. 11A,B). Pairs of cephalic trichobothria are not recognisable. The triangular vertex (vx) is not clearly separated from the flattened frons (fr) (Fig. 11A). The frons is separated from the clypeus by the epistomal ridge (epr) (Fig. 11B), which is less distinct than in *Systelloderes*. The compound eyes are located laterally, composed of fewer ommatidia than in *Systelloderes* and restricted to the posterior part of the head, close to the anterior margin of the prothorax (Fig. 11B). A thin sclerotised plate separates the anteromesal side of the eye from the adjacent region of the head capsule (indicated by arrows in Figs. 12A, 16G). The circumocular ridge (cor) is indistinct. Ocelli are absent. The genal area (ga) is adjacent to the anteroventral region of the compound eye (Fig. 11B). The anterior region of the head capsule is transformed into a ring-like bulge representing the bucculae (bu) (Figs. 11B,C, 16C–E). The antennal socket (as) lies between the bucculae and the genal area (Figs. 11B, 16F). Setose maxillary and mandibular plates are present dorsad the bucculae, between the antennal base and the clypeus, respectively. The maxillary plates (mxpl) are blunt cone-shaped sclerites separated from the bucculae by the ventral cleft (vc, see PARSONS 1968) (Figs. 11B, 16C). The mesal areas are slightly protruding inwards and form the ventral guiding device for the feeding stylets (Figs. 12, 16C). Their posterior regions are fused with the head capsule (Fig. 16C,D). The lora or mandibular plates (lor) are similar in shape to the maxillary plates but more pointed dorsally. They are separated from the former by the mandibular sulcus (msu) and from the clypeus by the clypeoloral cleft (clc) (Figs. 11B, 16C). The mesal edges are attached to the hypopharynx while the caudal ones are fused with the head capsule (Fig. 16C,D). In contrast to *Systelloderes* the genal suture is not recognizable. The anterior and mesal regions of the maxillary and mandibular plates are both covered by the clypeus (Fig. 16C). Subgena, subgenal ridges and the frontal and coronal (= epicranial) sutures are not distinguishable.

The ventral closure of the head capsule is formed by the "gular region" (gu). It is separated from the bucculae by a rim (Fig. 11C). The gular region is glabrous, except for two setae located mesally in the same plane as the compound eyes (Fig. 11B,C).

The dorsolateral area of the short postoccipital region is completely retracted into the prothorax (Figs. 12, 16I). The postoccipital ridge is not distinguishable. In contrast to the enicocephalid species, this region of the head does not form a ball-and-socket joint. The thickness of the lateral sides of the postoccipital region is partly increased (stout paired cuticular condyles, indicated by an arrow in Fig. 16I). The dorsal side is not transformed into a thin lip-like apodeme. The ventral region of the postoccipital region ends with the anterior margin of the prothorax and is not covered by the latter (Fig. 11C). The cervix is re-

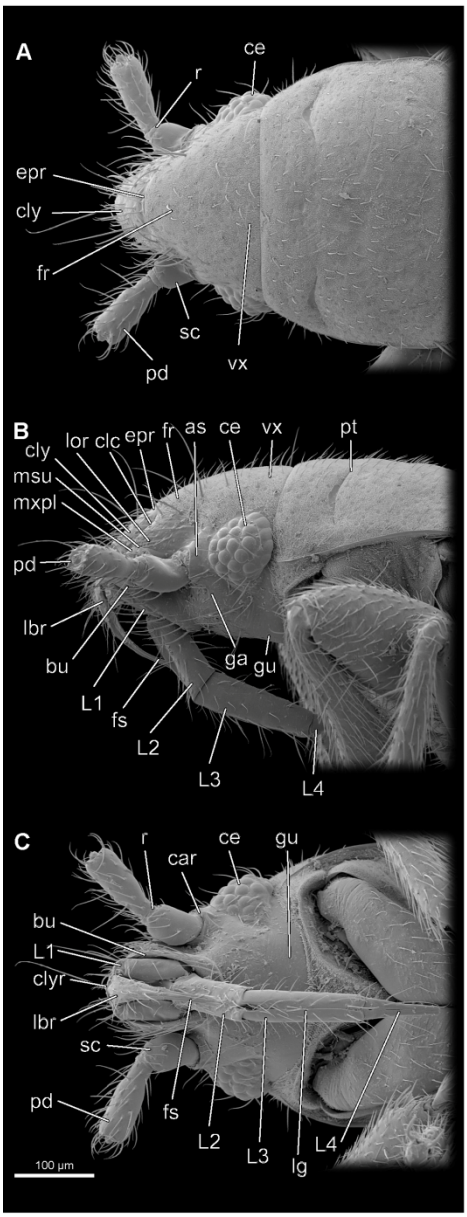

Fig. 11. *Cryptostemma waltli* Fieber, 1860: head and thorax, basi- and distiflagellum omitted, SEM. **A**: dorsal view; **B**: lateral view; **C**: ventral view. as, antennal socket; bu, buccula; car, circumantennal ridge; ce, compound eye; clc, clypeoloral cleft; cly, clypeus; epr, epistomal ridge; fr, frons; fs, feeding stylets; ga, genal area; gu, gular region; L1–L4, labial segment 1–4; lbr, labrum; lg, labial groove; lor, lorum/mandibular plate; msu, mandibular sulcus; mxpl, maxillary plate; pd, pedicellus; pt, prothorax; r, ring-like structure between scapus and pedicellus; sc, scapus; vx, vertex.

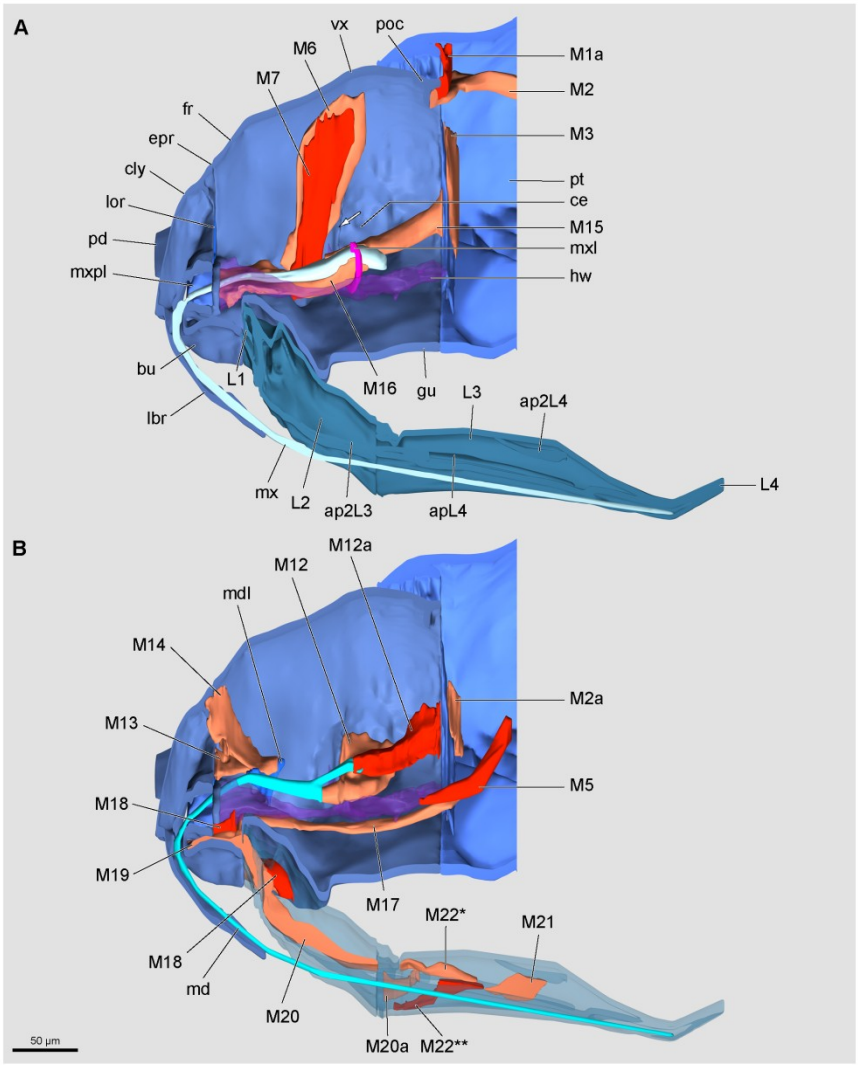

Fig. 12. *Cryptostemma waltli* Fieber, 1860: head and thorax, 3D-reconstruction, sagital section, different muscles and feeding stylets shown (blue: sclerotization, red: musculature), labium in (B) semitransparent. ap2L3, unpaired bar-shaped apodeme of the 3rd labial segment; apL4, paired apodeme of 4th labial segment; ap2L4, unpaired apodeme of 4th labial segment; b, buccula; ce, compound eye; cly, clypeus; epr, epistomal ridge; fr, frons; gu, gular region; hw, hypopharyngeal wing (semitransparent); L1–L4, labial segment 1–4; lbr, labrum; lor, lorum/mandibular plate; M, muscle with appropriate number (number of muscle corresponds to number in text, Figs. 14–16, Table 1); md, mandible; mdl, mandibular lever; mx, maxilla; mxl, maxillary lever; mxpl, maxillary plate; pd, pedicellus; poc, postoccipital region; pt, prothorax; vx, vertex. Arrow in (A) indicates sclerotised plate of compound eye (see also Fig. 16G).

duced. The pronotal collar (see Emsley 1969) is absent in *Cryptostemma*.

Musculature. (M1–M5). M1 not distinguishable in *Cryptostemma*. M1a (Figs. 12A, 16I): larger than in *Systelloderes*, O – mesal area of the pronotum; I – mediodorsal region of the postocciput; F – depressor of the head. M2 (Figs. 12A, 16I, J): O – mesonotum; I – dorsally on the postocciput; F – levator of the head. M2a (Figs. 12B, 16I): O – laterally on the pronotum; I – dorsomedially on the postocciput; F – levator of the head. M3 (Figs. 12A, 16I): O – mesal region of the pronotum; I – ventrolaterally on the postocciput; F – depressor of the head. M4

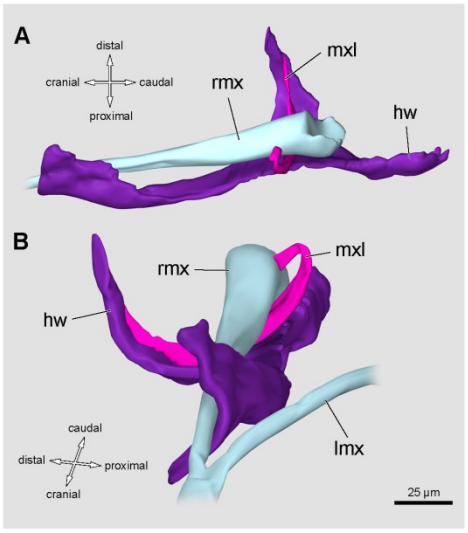

Fig. 13. *Cryptostemma waltli* Fieber, 1860: hypopharyngeal wing and maxillary lever, 3D-reconstruction. **A**: dorsolateral view; **B**: frontal view. hw, hypopharyngeal wing; lmx, left maxilla; mxl, maxillary lever; rmx, right maxilla.

absent. M5 (Figs. 12B, 16I, J): likely fused with M5b, O – anterad the profurcal arm; I – ventrally near the post-occipital region; F – depressor and retractor of the head. M5a absent.

Tentorium

The tentorium is completely reduced. Anterior and posterior tentorial pits are not developed. Endoskeletal elements not belonging to the tentorium are the hypopharynx, the hypopharyngeal wings, the piston of the salivary pump and the mandibular and maxillary lever, which are treated separately in the following chapters.

Clypeus and labrum

The rectangular and flat clypeus (cly) is not divided into an anteclypeus, paraclypeus and postclypeus. Its dorsal side is densely covered with long setae (Fig. 11A,B). The anterior part of its ventral region forms a longitudinal rim functioning as a guiding device for the stylets (Fig. 16B). Its posterior ventral region and the dorsal side of the hypopharynx together form a tongue-and-groove-joint (Fig. 16C).

In contrast to *Systelloderes*, the clypeus of *Cryptostemma* is directed more dorsoventrally (Figs. 11B, 12A). The triangular labrum follows this orientation. It is almost as long as the clypeus and bent in a ventrocaudal direction. The clypeo-labral ridge (clyr) is distinct (Fig.

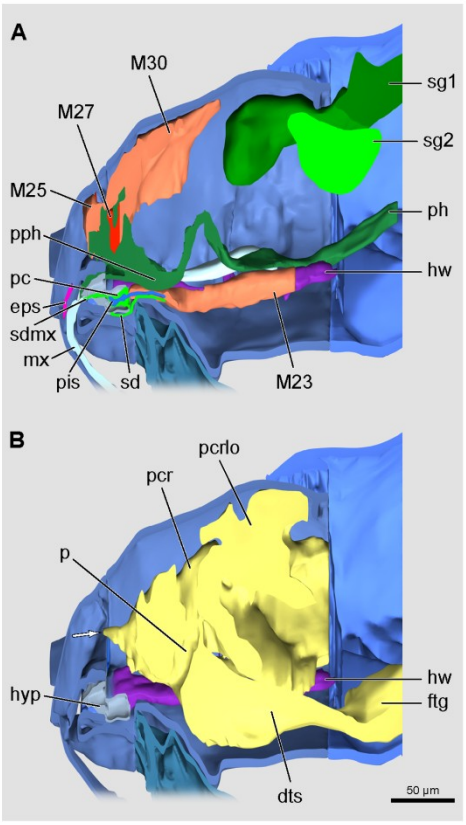

Fig. 14. *Cryptostemma waltli* Fieber, 1860: head and thorax, 3D-reconstruction, sagital section, different muscles, alimentary system (A) and nervous system (B) shown (blue: sclerotization, dark green: pharynx, light green: salivary complex, red: musculature, yellow: nervous system). dts, deuto-tritocerebrum-subesophageal-complex; eps, epipharyngeal sense organ; ftg, first thoracal ganglion; hyp, hypopharynx; M, muscle with appropriate number (number of muscle corresponds to number in text, Figs. 12, 15, 16, Table 1); mx, maxilla; p, passage through brain for pharynx; pc, pumping chamber; pcr, protocerebrum; pcrlo, protocerebral lobe; ph, pharynx; pis, piston; pph, prepharynx; sd, common salivary duct; sdmx, salivary duct connecting pumping chamber with salivary channel of maxillae; sg1, principal gland; sg2, accessory gland. Arrow in (B) indicates extension of protocerebrum (see also Fig. 16D).

11C). The dorsal side of the clypeus is densely covered with setae. The clypeal longitudinal guiding rim continues on the ventral side (Fig. 16B,C). Due to the hypognathous placement of the tip of the labium, the labrum is not attached to the first and second labial segments (as in *Systelloderes*). A large cleft is present between these structures (Fig. 11B).

Musculature. No muscles are associated with the clypeus and the labrum. M10 and M11 absent.

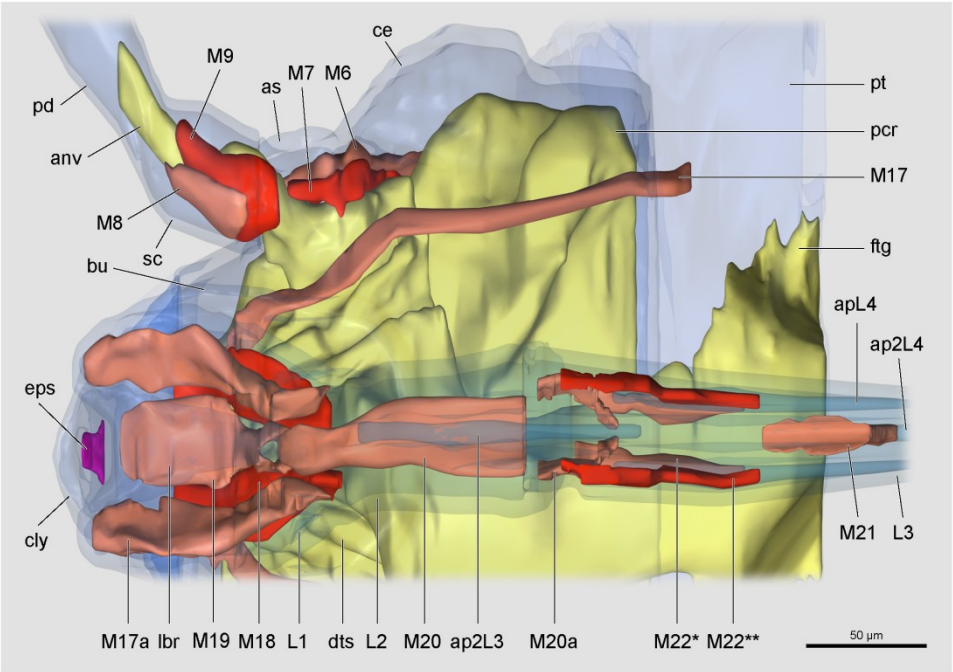

Fig. 15. *Cryptostemma waltli* Fieber, 1860: head and thorax (semitransparent), 3D-reconstruction, ventral view (blue: sclerotization, red: musculature, yellow: nervous system). anv, antennal nerve; ap2L3, unpaired apodeme of 3rd labial segment; apL4, paired apodeme of 4th labial segment; ap2L4, unpaired apodeme of 4th labial segment; as, antennal socket; bu, buccula; ce, compound eye; cly, clypeus; dts, deuto-tritocerebrum-subesophageal-complex; eps, epipharyngeal sense organ; ftg, first thoracal ganglion; L1–L3, labial segment 1–3; lbr, labrum; M, muscle with appropriate number (number of muscle corresponds to number in text, Figs. 12, 14, 16, Table 1); pcr, protocerebrum; pd, pedicellus; pt, prothorax; sc, scapus.

Antennae

The four-segmented antenna is inserted on an indistinct antennal socket (as). It is located anterad the compound eye (Fig. 11B). The circumantennal ridge is indistinct. An antennifer is absent. The scapus (sc) is cylindrical and sparsely covered with setae posteriorly and laterally. It is half as long as the pedicellus (Fig. 11B,C). "Scapus sclerites" (see 3.1. *Systelloderes* sp.) are not developed. The pedicellus (pd) is covered with setae on all sides (Fig. 11). A ring-like structure (r) is present between the tip of the scapus and the base of the pedicellus (Fig. 11). It likely represents the prepedicellite. It is distinct in SEM images but not recognizable in the corresponding histological sections (Fig. 16D). The very fragile flagellomeres were missing in the specimens available to us, but a detailed description of the antennae of Dipsocoromorpha was provided by Zrzavý (1990).

Musculature. Extrinsic and intrinsic antennal muscles (M6–M9). M6 (Figs. 12A, 15, 16G): O – roof of the head capsule, at the level of the compound eye; I – posterad the ventral base of the scapus; F – depressor of the antenna. M7 (Figs. 12A, 15, 16G): O – roof of the head capsule, mesad the O of M6; I – posterad the dorsal base of the scapus; F – levator of the antenna. M8 (Figs. 15, 16D): O – proximal base of the scapus; I – proximal base of the pedicellus; F – extensor of the pedicellus. M9 (Figs. 15, 16): laterad M8, O – distal base of the scapus; I – distal base of the pedicellus; F – flexor of the pedicellus.

Mandible

The mandibles (md) are a pair of symmetrical, long and slender stylets. One third of their entire length lies within the head capsule where their bases reach the region of the compound eye (Fig. 12B). The orientation of the proximal halves is approximately parallel to the longitudinal boxy axis while the distal parts are strongly bent caudad in their resting position (Fig. 12B). In contrast to *Systelloderes* the distal parts are ellipsoid in cross section and apparently do not enclose the maxillae (Figs. 16C–E). The hollow widened part anterad of the compound eye (Figs. 12B, 16G) is transformed into a sclerotised tendon on its dorsal side posteriorly with an irregular shape in cross section (Fig. 12A, 16H).

The sclerotised mandibular lever (mdl) is a stout right angle. The arm which is attached to the stylet is elongated (type II of RIEGER 1976) (Fig. 12B). It is located posterad the lorum and attached to the mandible by its simple anterior apex (Fig. 16E,F). A longitudinal sclerotised stripe of cuticle is not present. The mandibular sac is indistinct. Mandibular glands are absent.

Musculature. Retractor and promotors of the mandibular stylet (M12–M14). M12 (Figs. 12B, 16G, H): O – laterally on the roof of the head capsule, posterad the compound eye; I – posterad the widening of the mandible; F – retractor. M12a (Figs. 12B, 16H): O – laterally on the postoccipital region, near the thickening of the cuticle; I – slender apodeme of the mandible; F – retractor. M12b: absent. M13 (Figs. 12B, 16C–E): O – lorum; I – laterally on the distal side of the mandibular lever; F – protractor. M14 (Figs. 12B, 16D–F): O – dorsally on the border region of clypeus and head capsule; I – laterally on the distal side of the mandibular lever, posterad the I of M13; F – protractor.

Maxilla

The maxillae consist mainly of the very elongate laciniae. The palp and galea are absent. The proximal elements appear indistinguishably fused, without a recognizable detachment of the lacinia from the stipes. The laciniae, probably together with the parts corresponding with the cardo and stipes (mx), form a pair of hollow, slender stylets. They are similar to the mandibles in position and shape. However, they end abruptly posteriorly with their widened part (Figs. 12A, 16H). The linkage of the anterior two thirds resulting in the formation of the food channel and salivary channel is similar to that of *Systelloderes* (Fig. 16H). The E-shaped structure reaches the region posterad the antennal socket (Fig. 16F). The maxillary sac is not distinct. The posterior region of the maxilla is mesally connected with a crescent-shaped maxillary lever (Fig. 12A). The proximal part of this sclerotised structure is strongly bent laterad and attached to the mesal side of the maxilla, while the distal region follows the lateral extension of the hypopharyngeal wing (Figs. 13, 16H). Maxillary glands are not present.

Musculature. Retractor and promotor of the maxillary stylet (M15, M16). M15 (Figs. 12A, 16H, I): O – laterally on the distal postoccipital region, ventrad the increased sclerotization, ventrad the O of M12a; I – dorsally on the maxillary stylet, posterad the E-shaped structure; F – retractor. M16 (Figs. 12A, 16C, G, H): one of the largest intrinsic cephalic muscles, O – on the maxillary plate; I – ventrolaterally on the base of the stylet; F – promotor.

Labium

The tube-like, four-segmented labium forms the ventral closure of the anterior part of the head capsule (Fig. 11B,C). The feeding stylets lie within this tube (Fig. 12). In its resting position it is caudally oriented (Fig. 11B). In contrast to *Systelloderes* the entire surface of the labium is covered with a sparse vestiture of long setae (Fig. 11B,C). The labial groove (lg) is present on the ventral side of segments two to four (Fig. 16G). The four segments are separated from each other by articulation membranes (Fig. 11B,C). The basal segment (L1) is shorter than the others, only weakly sclerotised, and not in contact with the feeding stylets (Figs. 11B, 16C,D). Its ventral area is strongly folded and clearly separated from the second segment (Fig. 11C, 16A). The second (L2) and third segments (L3) are similar in shape. The base of L2 is partly retracted into the basal segment. In contrast to *Systelloderes*, no distinct apodemes are present. The third segment (L3) is the longest and 1.5 as long as L2 (Fig. 11B,C). Its base is partly retracted into L2 and bears an apodeme on both sides. The floor of the proximal labial groove is strongly sclerotised and forms a bar-shaped apodeme anteriorly as in *Systelloderes* (ap2L3) (Figs. 12A, 15, 16H). A distinct linkage of the edges of the labial groove is not present (Fig. 16H–J). The cone-shaped apical labial segment (L4) is half as long as L2 (Fig. 11C). Two bar-shaped apodemes (apL4) originate on its base and reach almost the distal end of L3 (Figs. 12A, 15, 16J). Additionally, an unpaired bar-shaped apodeme is present (ap2L4). It originates on the dorsal base of L4 and is attached to the dorsal side of the middle region of L3. A distinct apical row of sensilla is not present (Fig. 11C). Intercalary sclerites are also missing.

Musculature. Extrinsic and intrinsic labial muscles (M17–M22). M17 (Figs. 12B, 15, 16D): largest extrinsic labial muscle, O – ventrolaterally on the postoccipital region; I – distally on the base of L1; F – extensor of the labium. M17a (Figs. 15, 16B,C): O – anterior part of the bucculae; I – anterior base of L2; F – flexor of the labium (simultaneous contraction) or rotator. M18 (Figs. 12B, 15, 16D): O – anterior border region of the hypopharyngeal wing and the mesal wall of the maxillary plate; I – posterior base of L2; F – flexor of the labium (simultaneous contraction) or rotator. M19 (Figs. 15, 16C,E): unpaired, O – mesally on the anterior region of the bucculae L2; I – with its bifurcated posterior region on the anterior base of L2, mesad the I of M17; F – flexor of the labium. M20 (Figs. 12B, 15, 16F, H): unpaired, O – anterior base of L2, posterad the I of M19; I – dorsally on the base of L3; F – flexion of L3 and L4. M20a (Figs. 12B, 15): O – laterally on the base of L3; I – laterally on the posterior part of the apodeme ap2L3; F – contraction likely results in an extension of L2. M21 (Figs. 12B, 16J): unpaired, stout muscle, O – ventrally on the apodeme ap2L4; I floor of the labial groove in L3; F – pulls the floor of the labial groove upwards and closes the lateral sides of the labial groove, probably also extension of L4 (connection over the labial floor). M22* (Figs. 12B, 16I): first partition of M22, O – dorsally on the anterior side of L3; I – dorsally on the apodemes apL4; F – flexion (simultaneous contraction) or rotator of L4. M22** (Figs. 12B, 16I): second partition of M22, O – ventrolaterally on the anterior side of L3; I – ven-

trally on the apodemes apL4; F – flexion (simultaneous contraction) or rotator of L4.

Hypopharynx, salivary pump and salivary glands

The sclerotised hypopharynx (hyp) is subdivided into a three-cornered anterior part ("hypopharyngeal lobe") and a bowl-shaped posterior part (Fig. 14A). The former is dorsally enclosed by the clypeus, laterally by the mandibular and maxillary plates, and ventrally by the bucculae and the dorsal base of the first labial segment (Fig. 16C). The anterodorsal side of the hypopharynx forms a rim (Fig. 16C). In combination with the ventral extension of the clypeus, it forms the transition between the prepharynx and the food channel formed by the maxillary stylet. Its ventrolateral sides bear two paired indentations functioning as the dorsal guiding device for the feeding stylets (Fig. 16C). The duct connecting the pumping chamber with the salivary channel of the maxillae (sdmx) lies within the ventral hypopharyngeal region (Figs. 14A, 16C). The proximal areas of the anterior part are fused with the mesal walls of the maxillary plates laterally and the prepharynx dorsally (Fig. 16D). The posterior part encloses the membranous pumping chamber (pc) (Figs. 14A, 16D).

The hypopharyngeal wings (hw) are more complex than those in *Systelloderes*. They are formed by lateral extensions of the anterior hypopharyngeal part (Fig. 16C,D). The mesoventral wall of the maxillary plate and the ventral wall of the lorum are partly integrated in the anterior region of the wings, the latter on the dorsal side (Fig. 16D). Consequently, the wings have a dorsoventral orientation in this region of the head (Figs. 13B, 16D). The two lateral rims of the hypopharynx are guiding devices for the feeding stylets, with the posterior part interacting only with the maxillae (Figs. 13A, 16D,E). Anterad the compound eyes the orientation of the hypopharyngeal wings switches from dorsoventral to transverse (Figs. 13A, 16G). In the ocular region, the wing is more planar and forms a triangular extension laterally which is directed dorsad and located close to the internal ocular plate (Figs. 13, 16G, H). In its posterior region the wing tapers and switches back to a dorsoventral orientation (Figs. 13B, 16I). Its posterior end is located in the border region of the head capsule and prothorax (Figs. 14B, 16I).

The structure of the functional complex of the salivary pump is similar to that of *Systelloderes*. However, the duct "sdmx" in *Cryptostemma* is located more ventrally in relation to the hypopharynx. The connection between the salivary duct "sd" and the principal gland (sg1), the principal duct and the accessory duct could not be reconstructed precisely with the available section series (Fig. 14A). The sac-shaped elongated principal gland (sg1) is composed of few large cells and situated in the border region between the head capsule and prothorax (Figs. 14A, 16H, J). The cells are densely filled with secretion granules (se) which enclose a bean-shaped large nucleus (n) (Fig. 16H). The thin tunica propria (tp) forms the external layer (Fig. 16H). A second gland (sg2) of vesicular structure, possibly homologous with the accessory gland, is present posteroventrad the principal gland. According to Miyamoto (1967) it is located "below the principal gland". This gland is also sac-shaped but composed of smaller cells. Associated nerves are not recognizable.

The sclerotised piston (pis) is similar to that of *Systelloderes* (Fig. 14A). However, the posterior end is blunt and not bifurcated. The transition of the ovoid part to the plate-like part is smooth without a distinct folding in cross section (Fig. 16E).

Musculature. M23 (Figs. 14A, 16E, H): one of the largest muscles of the head, O – mesal side of the posterior and middle region of the hypopharyngeal wing; I – laterally on the middle region of the piston; F – contraction results in an extension of the pumping chamber and influx of saliva from the salivary glands; relaxation pulls the piston back into the pumping chamber, thus pumping saliva through the salivary duct (sdmx) to the maxillary salivary channel. M24 absent.

Epipharynx

The epipharynx is not present as a clearly defined structural unit. It may be represents a flat area of the caudal clypeal region. The density of the tissue in the anteroventral clypeal region is distinctly higher than in the surrounding areas. This flattened agglomeration of cells likely represents the epipharyngeal sense organ (eps) (Figs. 14A, 15, 16B).

Musculature. No muscles are directly associated with the epipharynx.

Pharynx

The cephalic digestive tract is divided into two regions which distinctly differ morphologically and histologically. The short precerebral part, i.e. the prepharynx, has a wide lumen and reaches from the origin of the maxillary food channel to the level of the antennal socket (prepharynx, pph) (Fig. 14A). As in *Systelloderes* it is V-shaped in cross section with a sclerotised ventral floor and a membranous dorsal wall with a strongly sclerotised tendon attached to it (Fig. 16C–E). The prepharynx is partly covered by the protocerebrum (pcr) dorsally (Fig. 16F). The transition to the tube-shaped pharynx (ph) is enclosed by the anterior part of the brain and surrounded by a delicate ring muscle layer (Fig. 16G). In this region the pharynx is strongly bent and appears like a reversed "V" in cross section (Fig. 14A). The posterior pharyngeal section is shifted to the right side of the head whereas the esophagus lies in the median plane in the thoracic segments (Figs. 14A, 16I).

Musculature. Pharyngeal muscles (M25–M30). Longitudinal muscles not recognizable. M25 (Figs. 14A,

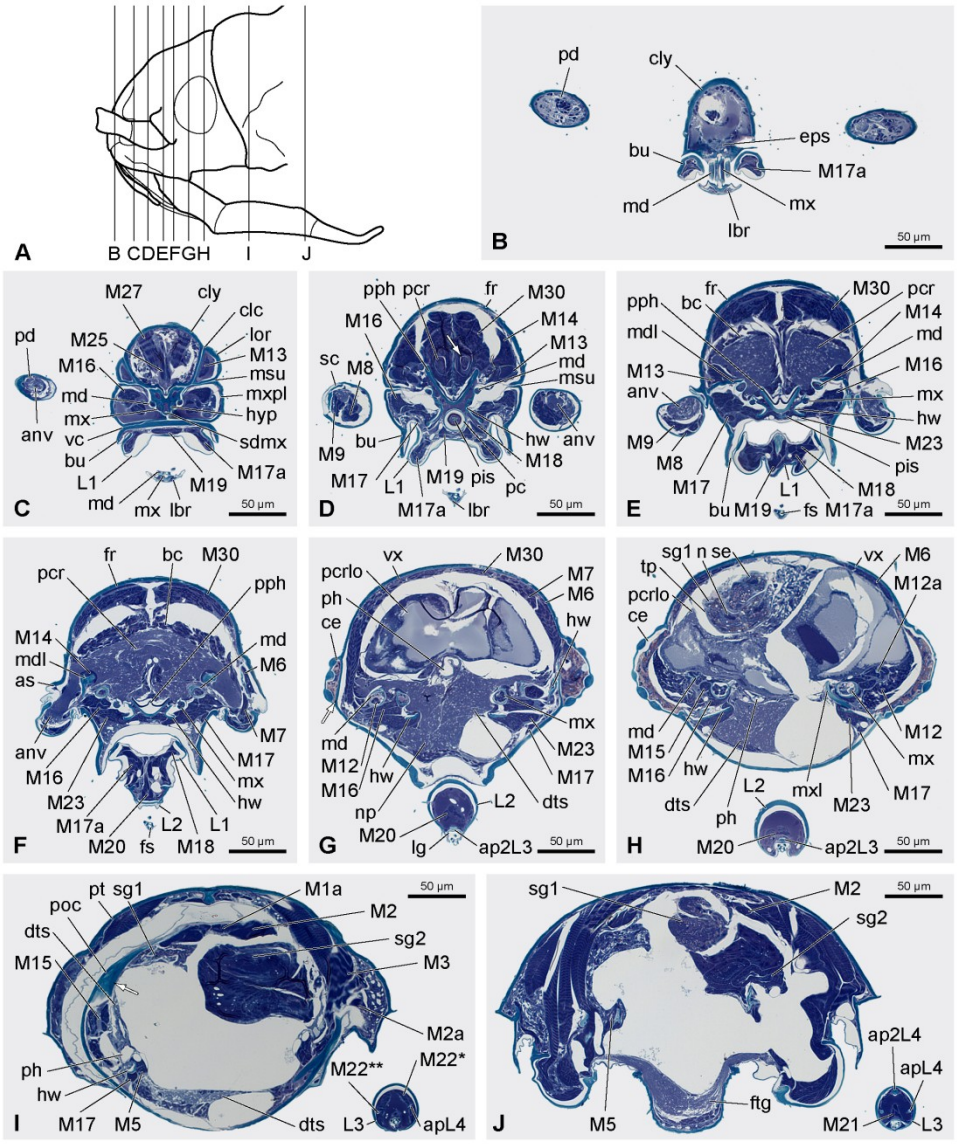

Fig. 16. *Cryptostemma waltli* Fieber, 1860: head and thorax, cross sections. **A**: head and thorax, basi- and distiflagellum omitted, schematic, lateral view showing planes of section of light micrographs **B**–**J**: C: left antenna omitted; I, J: labium displaced dorsolaterally. anv, antennal nerve; ap2L3, unpaired apodeme of 3rd labial segment; apL4, paired apodeme of 4th labial segment; ap2L4, unpaired apodeme of 4th labial segment; as, antennal socket; bc, bark cell; bu, buccula; ce, compound eye; clc, clypeoloral cleft; cly, clypeus; dts, deuto-tritocerebrum-subesophageal-complex; eps, epipharyngeal sense organ; fr, frons; fs, feeding stylets; ftg, first thoracal ganglion; hw, hypopharyngeal wing; hyp, hypopharynx; L1–L3, labial segment 1–3; lbr, labrum; lg, labial groove; lor, lorum/mandibular plate; M, muscle with appropriate number (number of muscle corresponds to number in text, Figs. 12, 14, 15, Table 1); md, mandible; mdl, mandibular lever; msu, mandibular sulcus; mx, maxilla; mxl, maxillary lever; mxpl, maxillary plate; n, nucleus; np, neuropil; pc, pumping chamber; pcr, protocerebrum; pcrlo, protocerebral lobe; pd, pedicellus; ph, pharynx; pis, piston; poc, postoccipital region; pph, prepharynx; pt, prothorax; sc, scapus; sdmx; salivary duct connecting pumping chamber with salivary channel of maxillae; se, secretion granules; sg1, principal gland; sg2, accessory gland; tp, tunica propria; vc, ventral cleft; vx, vertex. Arrow in (D) indicates extension of protocerebrum (see also Fig. 14B). Arrow in (G) indicates sclerotised plate of compound eye (see also Fig. 12A). Arrow in (I) indicates partly increased thickness of lateral sides of postoccipal region.

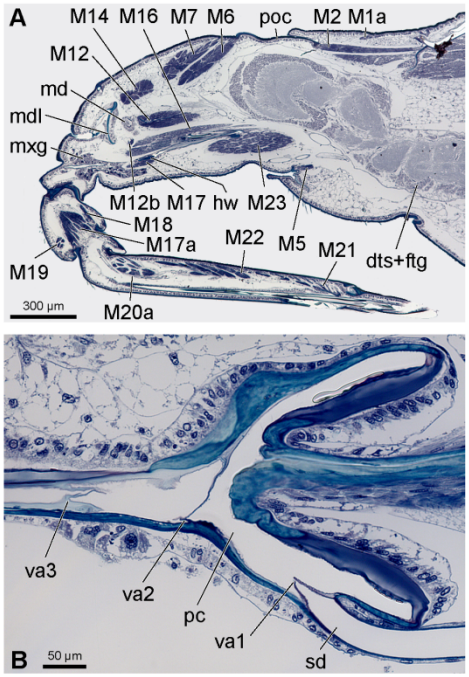

Fig. 17. *Gerris* sp.: **A**: head and thorax, right half, parasagittal longitudinal section. **B**: detail of salivary pump, sagittal longitudinal section. dts+ftg, fused complex of deutocerebrum, tritocerebrum, subesophagealganglion and first thoracic ganglion; hw, hypopharyngeal wing; M, muscle with appropriate number (number of muscle corresponds to number in text and Table 1); md, mandible; mdl, mandibular lever; mxg, maxillary gland; pc, pumping chamber; poc, postoccipital region; sd, afferent salivary duct; va, valve with appropriate number.

16C): unpaired, V-shaped, O – dorsally on the posterior region of the clypeus; I – dorsally on the prepharygeal tendon; F – dilator of the cibarium. M26 not distinguishable as a separate unit. M27 (Figs. 14A, 16C): unpaired, V-shaped, O – dorsally on the posterior region of the clypeus, posterad the O of M25; I – dorsally on the prepharygeal tendon, posterad the I of M25; F – dilator. M28 absent. M29 absent. M30 (Figs. 14A, 16D, G): unpaired, interrupted by two extensions of the protocerebrum anteriorly, O – frontal region; I – dorsally on the middle region of the prepharynx; F – dilator.

Brain

Due to the very small size of the head the brain appears greatly compressed. As in *Systelloderes* it is subdivided into the protocerebrum (pcr) and a compact complex comprising the deuto- and tritocerebrum and the subesophageal complex (dts) (Fig. 14B).

The protocerebrum (pcr) is composed of two extensions anterad which are likely the origin of the innervation of the epipharyngeal sense organ (Figs. 14B, 16D, indicated by arrows) and two dorsal lobes (pcrlo) covering the proximal region of the brain (Figs. 14B, 16G). The latter are caudally directed and reach the postoccipital region (Fig. 14B). In contrast to *Systelloderes* the narrow passage for the pharynx is very short. The circumesophageal connectives are not distinguishable. The optic lobes are indistinguishably fused with the lateral sides of the protocerebral lobes (Fig. 16H). The globular unit formed by the deuto- and tritocerebrum and the subesophageal complex (postcerebral complex, dts) is distinctly separated from the first prothoracal ganglion (ftg) by short and flat, mesally fused connectives (Fig. 16G–J). The paired antennal nerves (anv) arise from the anterior region of the postcerebral complex (Figs. 15, 16F). The frontal ganglion and the hypocerebralganglion are not recognizable as separate structures. Maxillary, mandibular and labial nerves could not be reconstructed precisely with the available section series.

As in *Systelloderes*, the thin neural lamella forms the external cell layer of the brain. The neurilemma is composed of single flattened cells and is even more sparsely developed than the one in *Systelloderes*. A bark cell layer (bc) of variable thickness encloses the dense internal neuropil (np) (Fig. 16E–G). The bark cell layer is very distinct in the anterodorsal region of the protocerebrum and the caudal lobes and reduced to few scattered cells in the proximal parts of brain. The density of the neuropil is uniform in the different parts of the brain.

Aorta cephalica and antennal hearts

Not clearly recognizable in the available section series, possibly reduced.

3.3. *Gerris* sp. (Gerromorpha)

The external and internal cephalic morphology was already described in detail in Matsuda (1961) and Andersen (1982). Consequently, we only present missing information here, especially on the muscle system (Fig. 17A). The cephalic muscles are numbered following the system used for *Systelloderes* and *Cryptostemma* (see Table 1). A distinctive feature of the salivary pump is the presence of three valves (Fig. 17B, va1–va3). The first valve (va1) is composed of two anteriorly directed flaps. They are placed at the anterior end of the common afferent salivary duct (sd) where it merges with the pumping chamber. The second valve (va2) on the floor of the salivary pump is formed by a large dorsal flap and a very small ventral one. Both are also anteriorly directed. The third pair of valve flaps (va3) is inserted directly anterior to the origin of the salivary duct, which is connected to

the salivary canal of the maxilla. Both are posteriorly directed. The valves obviously function passively as muscles are lacking.

4. Discussion

4.1. Morphology and homology

Systelloderes, *Cryptostemma* and *Gerris* differ strongly in their external and internal head morphology even though some heteropteran ground plan features are preserved in all three groups. We compared skeletal and muscular features potentially relevant in a phylogenetic context to conditions found in other heteropteran groups (Tables 1, 2) using extensive literature data (see Table 3). Antennal features were adopted from ZRZAVÝ (1990) and features of the digestive tract from MIYAMOTO (1961). Information on the feeding stylets was provided by COBBEN (1978).

Inconsistent designations for different cephalic areas were used by different authors dealing with Heteroptera (see below, e.g. "postclypeus"). Consequently we strictly follow the terminology used for head structures in SCHUH & SLATER (1995) and in a detailed study on the generalized Grylloblattodea (WIPFLER et al. 2011). The head of Hemiptera is generally composed of the vertex, the variously shaped frontoclypeal region, semicircular to quadrangular mandibular plates, triangular maxillary plates, mandibular and maxillary stylets, the tube-like labial rostrum, and a triangular labrum (SINGH 1971; SCHUH & SLATER 1995). Enicocephalomorpha are the only infraorder with the head capsule distinctly constricted behind the compound eyes which is combined with a distinctly swollen portion bearing the ocelli (autapomorphy) (see also WHEELER et al. 1993). The subdivision of the clypeus in ante-, post- and paraclypeus is indistinct in *Systelloderes*, Dipsocoromorpha, Ochteridae (RIEGER 1976), Gerromorpha (MATSUDA 1960; ANDERSEN 1982), Nepidae (Nepomorpha) (HAMILTON 1931) and Saldidae (PARSONS 1962), whereas the substructures are very clearly separated in other families such as for instance Corixidae (BENWITZ 1956: paraclypeal structures as "Clypeus-Seitenflügel"). The "postclypeus" of *Saldula* (PARSONS 1962), *Gerris* (Gerridae) (CRANSTON & SPRAGUE 1961), Gerromorpha (ANDERSEN 1982) and Schizopteridae (Dipsocoromorpha) (EMSLEY 1969) is in fact the morphological frons, and consequently the "frons" in *Saldula* (PARSONS 1962) is the vertex in the stricter sense (according the sequence from cranial to caudal: labrum, clypeolabral ridge, anteclypeus fused with postclypeus, epistomal ridge, frons, vertex). Assuming that, the epistomal ridge is homologous to the "clypeal fold" in Schizopteridae (EMSLEY 1969), to the

Table 1. Proposed homology of the musculature of *Systelloderes*, *Cryptostemma* and *Gerris* with other representatives of Hemiptera. Unclear homologies set in parentheses, (---) muscle absent, (?) not mentioned by the author or further figures and descriptions for a clear conclusion are absent in the cited works. [2] "T" referring to number of musculature of thorax, "H" referring to number of musculature of head. [3] Muscles were not named in BENWITZ (1956); therefore, the nomenclature of the enicocephalid species is applied.

Systelloderes	*Cryptostemma*	*Ochterus* (RIEGER 1976)	*Corixa* (BENWITZ 1956)	*Gelastocoris* (PARSONS 1958, 1959, 1960a)	*Lethocerus* (PARSONS 1968)	*Nepa* (HAMILTON 1931; RIEGER 1976)	*Gerris*	*Hydrometra* (SPRAGUE 1956)	*Saldula*[2] (PARSONS 1962, 1963)	*Triatoma* (BARTH 1952a,b, 1953a,b; RIEGER 1976	*Dysdercus* (KUMARI 1955; KHAN 1972)	*Hackerella* (SPANGENBERG et al. 2013)	*Aphis* (WEBER 1928, 1929)
M1	M1	TM10b	rot cap1	TM10b	10	?	M1	M3	T10	?	?	M1	Odvm
M1a	M1a	TM1	ret cap1	TM1	1	2nd cranial flexor	M1a	M2	T1	?	?	M1a	—
M2	M2	TM3	ret cap2	TM3	3	?	M2	M1	T3	?	?	M2	Odlm
M2a	M2a	TM10a	rot cap2	TM10a	6a	?	M2a	M7	—	?	?	—	—
M3	M3	TM2	depr cap	TM2	2	cranial flexor	M3	M10	T2	?	?	(M3)	Oism
—	—	—	—	—	—	?	—	—	—	?	?	M4	m.tent2
M5	M5	TM6	ret cap3	TM6	6B	?	M5	M6	T6	?	?	M5	Ovlm4
—	—	KM24	0 mu	KM24	H24	?	—	?	—	?	?	M5a	—
M5b	M5b	TM7	lev cap	TM7	7	?	M5b	M6	T7	?	?	—	Ovlm4
M6	M6	KM21	dep rsc	KM21	21	?	M6	?	H21	MU14	depressor	M6	ant1
M7	M7	KM20	lev?sc	KM20	20	?	M7	?	H20	MU13	levator	M7	ant4
M8	M8	KM23	M8[3]	KM23	H23	?	M8	?	H23	?	intrinsic muscles	M8	ant2

M9	M9	KM22	M9[3]	KM22	—	?	M9	?	H22	?	intrinsis muscles	M9	ant3
—	—	(TM11)	—	—	—	?	—	?	—	—	—	M10	—
—	—	—	—	—	—	?	—	?	—	—	—	M11	m. lam. mand1+2
M12	M12	KM10	retr mand	KM10	H10	KM10	M12	?	H10	—	retractors/*RMD1*	M12	m. retr. mand1+2
M12a	M12a	KM11	—	KM11	H11	—	M12a	?	H11	MU11	retractors/*RMD2*	—	—
M12b	—	—	—	—	—	?	M12b	?	—	—	—	—	—
M13	M13	KM8	protr mand	KM8	H8	KM8	M13	?	H8	MU15	protractors/ *PMD*	M13	m. protr. mand
M14	M14	KM9	—	KM9	—	—	M14	?	H9	MU8	—	M14	—
M15	M15	KM13	retr max	KM13	H13	KM13	M15	?	H13	MU9+ MU10	retractors/*RMX*	M15	m. retr.maax1+2
M16	M16	KM12	protr max	KM12	H12	KM12	M16	?	H12	MU6+ MU7	protractors/ *PMX1+2*	M16	m. protr. max1+2
M17	M17	KM2b	add lb1	—	H2B	KM2b	M17	?	H2	MU5	*ADL1*	M17	m. add1
M17a	M17a	KM1	MuFa	KM1	H1	KM1	M17a	?	H1	MU16	*(ABL)*	—	m. abd1+2
M18	M18	KM2a	add lb2	KM2	H2A	KM2a	M18	?	H1.5	MU4	*(ABL)*	M18	m. add2
M19	M19	KM3	depr lb1	KM3	H3B	KM3	M19	?	H3	—	—	M19	m. add4
—	—	—	—	—	H3A	?	—	?	—	—	?	—	—
M20	M20	KM4	—	KM4	H4	KM4	M20	?	H4	MU0 proximal	*ADL2*	M20	m. add3
M20a	M20a	KM5	trans lb	KM5	H5	KM5	M20a	?	H5	—	*ADL3*	—	m. trans2-4
M21	M21	KM6	—	KM6	H6	KM6	M21	?	H6	MU0 distal	*TLB1*	M21	m. trans5
M22*	M22*	KM7a	(depr lb2)	KM7	H7	KM7	M22*	?	H7	MUL	*RLB*	M22	m. abd3
M22*	M22*	KM7b	(depr lb2)	KM7	H7	KM7	M22**	?	H7	MUL	*RLB*	M22	m. abd3
M23	M23	KM25	retr pist	KM25	H25	KM25	M23	?	H25	MU12	*DSI1+2*	M23	m. retr. pist2
—	—	—	—	—	—	?	—	?	—	—	—	M24	(m. dil. cup1)
M25	M25	KM14	abd lr	KM14	H14	KM14	M25	?	H14	MU1	—	M25	m. dil1
M26	M26	KM15	dil cib	KM15	H15	KM15	M26	?	—	MU2	*DSP1*	M26	m. dil2
M27	M27	KM16	dil buc	KM16	H16	KM16	M27	?	H16	MU2	*DSP2*	M27	m.dil3
—	—	KM19	dil ph3 d	KM19	H19	?	—	?	H19	MU17	?	M28	—
—	—	KM18	dil ph 3 v	KM18	H18	?	—	?	H18	—	?	M29	m. depr. phar.
M30	M30	KM17+ KM17a	dil ph1 +2+m dilatator oris	KM17+ KM17	H17+ H17a	KM17+ KM17a	M30	?	H17+ H17a	MU3	*DPH*	M30	—
—	—	—	—	—	—	—	—	?	—	—	?	—	m. tent1
—	—	—	—	—	—	—	—	?	—	—	?	—	m. protr. max1
—	—	—	—	—	—	—	—	?	—	—	?	—	m. retr. pst1
—	—	—	—	—	—	—	—	?	—	—	?	—	m. dil. cup2
—	—	—	—	—	—	—	—	?	—	—	?	—	m. dil. cup3
—	—	—	—	—	—	—	—	?	—	—	?	—	m. dil. cup4
—	—	—	—	—	—	—	—	?	—	—	?	—	m. dil. cup5
—	—	—	—	—	—	—	—	?	—	—	?	—	m. 1trans1
—	—	—	—	—	—	—	—	?	—	—	?	—	m. add5
—	—	—	—	—	—	—	—	?	—	—	?	—	Ovlm1
—	—	—	—	—	—	—	—	?	—	—	?	—	Ovlm2
—	—	—	—	—	—	—	—	?	—	—	?	—	Ovlm3

"clypeal cleft" in Gerromorpha (Andersen 1982, see also his statement on page 31: "[…] divide the clypeal region into an anteclypeus […] and a postclypeus ([…] "frons" of many authors).") and to the "frontal suture" in *Gerris* (Cranston & Sprague 1961). In *Saldula* (Parsons 1962) the border of frons ("postclypeus") and clypeus ("anteclypeus") is indicated in fig. 3 but not labeled. The bucculae usually partly enclose the base of the labium. In *Saldula* ("gular lobe") (Parsons 1962) they are vestigial and completely absent in Enicocephalidae, Corixidae (Benwitz 1956), Gerromorpha (Andersen 1982). Genae partially reaching beyond the maxillary plates anteriorly probably only occur in Enicocephalidae and Reduviidae (Weirauch 2008). An apomorphic feature generally characterizing Heteroptera (autapomorphy) is the presence of a gula (e.g. Spooner 1938).

The median ocellus is always missing, whereas absence or presence of the paired ocelli varies among and within the higher groups of Heteroptera. Both character states occur for instance in Schizopteridae (Dipsocoromorpha) (Emsley 1969), Enicocephalomorpha (Štys 1995a) and Gerromorpha (Andersen 1982), and are frequently, but not always, correlated with a shortening of the hemelytron (brachypterous to apterous).

The postoccipital condyles are usually well developed, but reduced in *Hydrometra* (Sprague 1956) and *Dysdercus* (Kumari 1955; Khan 1972). According to Griffith (1945) they are vestiges of the cervical sclerites, whereas Hamilton (1981) interpreted the two ventral spurs as "posterior tentorial bars". We follow Rieger (1976) and Andersen (1982) who interpreted them as simple extensions of the postoccipital region.

The homology of the "dorsal apodemes" of *Saldula* (Parsons 1962) is ambiguous. Their specific position suggests that they may represent anterior tentorial arms. Accordingly, the corresponding indentations in *Saldula* (Parsons 1962), the small pits associated with the clypeal connectives ("sclerotised connections […] which run from the clypeus to the dorsolateral margins of the [foodpump]") in *Gelastocoris* (Parsons 1959), and the vestigial anterior pits in *Lethocerus* (Parsons 1968) may be identified as anterior tentorial grooves. The hypopharyngeal wing of *Nepa* is flanked by an additional paired sclerotised structure referred to as "anterior arm of tentorium" (Hamilton 1931). Its relative position suggests that it may be in fact homologous with the anterior arm. However, the assumed anterior arms do not originate on the epistomal ridge (= "frontal suture" of Hamilton 1931) but laterally between the clypeus and lora.

Three pairs of cephalic trichobothria are present in Leptopodomorpha, Gerromorpha and in some groups of Cimicomorpha (Schuh & Slater 1995). An additional fourth pair is present in Gerridae, arguably an autapomorphy of the family. The gerromorph cephalic trichobothria clearly differ from the "usual" flat articulation by their origin in a deep funnel-shaped pit (autapomorphy) (Andersen 1982) (character **12** in the phylogenetic analysis). Weirauch (2012) documented "three pairs of very long and stout setae" for the dipsocoromorph species *Vorago-coris schuhi* Weirauch (Schizopteridae). However, they differ not distinctly from the surrounding setae and are arguably no cephalic trichobothria in a stricter sense.

The antenna of Heteroptera varies considerably in its shape and composition. In the ground plan it is composed of four elongate tubular segments separated from each other by intraflagelloides (Zrzavý 1990). The preflagelloides (pedicello-flagellar intersegmental sclerites) also occur in Thysanoptera and Coleorrhyncha (Zrzavý 1990), but they are extremely reduced or absent in *Hackeriella* (Spangenberg et al. 2013). Although the antenna of Enicocephalomorpha is largely conforming to the assumed ancestral state, the condition of the prepedicellite and its affiliation to the ground plan remains uncertain. It is absent in Nymphocorinae and Alienatinae (see Zrzavý 1990). So far, the "scapus sclerites" are only documented for *Systelloderes* which is treated here (autapomorphy). According to Zrzavý (1990), there are two antennal synapomorphies for Dipsocoromorpha – "the preflagelloid of type IV and the tubulous extension of the pedicellar apex into the pedicello-flagellar articulation". A ring-like desclerotised region of the basiflagellite and distiflagellite ("R-structure") occurs in Dipsocoromorpha, Gerromorpha, Leptopodomorpha and Cimicomorpha (Zrzavý 1990). However, its shape is highly variable in Dipsocoromorpha and Gerromorpha and it can be absent in the former. Apparently, the entire antennal morphology is of limited value for phylogenetic reconstruction on a higher level due to its extreme variability within the infraorders.

Hydrometra and *Systelloderes* are the only taxa with the retractor muscles of the piston originating on the posterior cephalic region. This is likely due to the extremely elongated head and the limited capacity of the hypopharyngeal wings to extend.

The presence of maxillary glands in the ground plan of Heteroptera is questionable (Schuh & Slater 1995). They are absent in *Systelloderes*, *Cryptostemma*, *Hydrometra*, *Saldula*, and *Triatoma*. The presence of mandibular glands in the ground plan of Heteroptera is also questionable. They are documented for *Oncopeltus* (Lygaeidae, Pentatomomoprha) (Linder 1956) and also for some Aphididae (Saxena & Chada 1971).

Triturating devices of the food pump for crushing and grinding particles in the food stream occur only in infraorders mainly or exclusively containing carnivorous species. However, they are absent in the predacious *Systelloderes*, *Cryptostemma*, *Gerris*, *Hydrometra* and the blood-feeding *Triatoma*. According to Cobben (1978) it is unclear why some groups evolved these nodes and ridges and others apparently did not.

The homology of cephalic muscles of members of Heteroptera and the other hemipteran lineages is still greatly impeded by a severe lack of reliable data, especially for Auchenorrhyncha. In the following, selected ambiguous muscles of representatives of Heteroptera, Coleorrhyncha (*Hackeriella*) and Sternorrhyncha (*Aphis*) are discussed, based on the results presented here, the detailed treatment of the head morphology of *Hacke-*

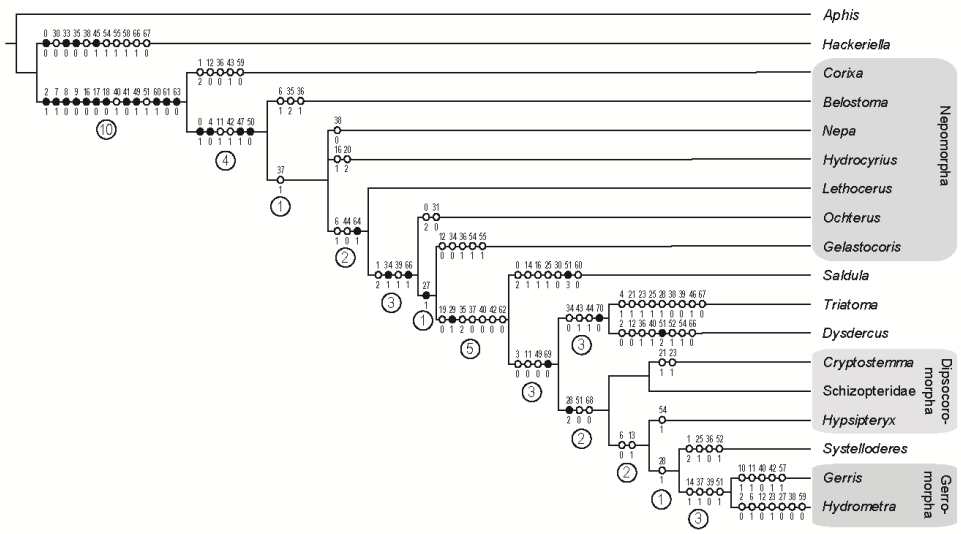

Fig. 18. Phylogenetic diagram [16 heteropteran taxa and *Aphis* (Sternorrhyncha) and *Hackeriella* (Coleorrhyncha)] generated with nona and tree analyses using new technology (single minimum length tree). Full circles show unambiguous apomorphic character states, white circles show homoplasious changes and encircled numbers give Bremer support values. The numbers correspond to those in chapter 4 and Table 2.

riella in Spangenberg et al. (2013), and previously published anatomical studies on members of Heteroptera and *Aphis*. The homology of **M3** (M. pronoti secundus, terminology of Parsons 1959, 1960a and Rieger 1976) of Heteroptera and Coleorrhyncha (*Hackeriella*) is problematic. The muscle originates on the pronotum and inserts on the posterior margin of the head capsule in Heteroptera (and *Aphis*), but on the apodeme of the maxillary plate in *Hackeriella*. The homology would imply a shift of the insertion. **M5a** (M. dilatator oris glandulae capitis) of *Hackeriella* is likely equivalent to the dilatator muscle of the maxilliary gland in Heteroptera. The gland is probably generally absent in Coleorrhyncha, and the muscle is a vestigial unpaired structure. Nevertheless, the similar position suggests homology. The labial abductor muscles ABL of *Dysdercus fasciatus* are located in a similar position as **M17a** and **M18**. However, the description in Khan (1972) does not allow an unambiguous interpretation. Khan (1972) documented transverse muscles TLB2 in the fourth labial segment of *Dysdercus fasciatus*. These are apparently very small fibers distinctly differing from muscles functioning as a compact unit. They are also present in the enicocephalid species but extremely small. The interpretation of the labial muscles of *Corixa* is complicated by the reduced structure of the labium. This applies for instance to the depr lb2 (m. depressor labii secundus) which may or may not be homologous with **M22** (M. retractor segmenti ultimi labii). Both **M24** of Coleorrhyncha and m. dil. cup1 (m. dilatator primus cupulae) of *Aphis* originate on the hypopharynx (Weber 1928), which suggests possible homology. However, in contrast to the condition in *Aphis* M24 inserts on the afferent common salivary channel and not directly on the pumping chamber. The homology of the two muscles would imply a shift of insertion in *Hackeriella*. As already stated in Spangenberg et al. (2013), the structure of the musculature of the food pump is highly variable and the separation of defined sets of muscles (M25–M27, M30) is difficult (i.e. fig. 15 in Parsons 1968). In particular this concerns the subdivision or fusion of the two partitions of **M30** (M. dilatator cibarii quartus). Therefore, we treat the posterior set of the cibarial retractors as a single morphological entity.

A hypothesis on homology of muscles listed and named in the systems of von Kéler (1963), Friedrich & Beutel (2008), and Wipfler et al. (2011) was already presented in Spangenberg et al. (2013) and is shown here in Table 1.

4.2. Phylogeny and character evolution

A cladistic analysis based on 71 head characters of 16 heteropteran terminals and *Hackeriella* and *Aphis* as outgroups (Table 2) yielded two minimum length trees (L: 175) with the strict consensus (L: 176) as shown in Fig. 18. Apart from the well supported monophyly of Heteroptera, the branching pattern is in contrast to other currently favored hypotheses. Some results, in particular the

Table 2. Character states of adults of selected taxa of Heteroptera with the outgroups *Aphis* and *Hackeriella* (below on this page; numbers correspond to those in text and Fig. 18), and List of Characters (following page).

	0 0	1 0	2 0	3 0	4 0	5 0	6 0	7 0	8 0	9 0	0 1	1 1	2 1	3 1	4 1	5 1	6 1	7 1	8 1	9 1	0 1	1 2	2 2	3 2	4 2	5 2	6 2	7 2	8 2	9 2	0 2	1 3	2 3	3 3	4 3	5 3
Sternorrhyncha: *Aphis*	2	1	0	–	1	0	0	0	1	1	0	0	1	1	0	–	1	1	1	0	0	0	–	0	–	0	–	0	–	?	1	0	0	1	4	1
Coleorrhyncha: *Hackeriella*	0	0	0	–	1	1	0	0	1	1	0	0	1	1	0	–	1	1	1	1	2	0	–	–	–	0	–	0	–	–	0	0	0	0	–	0
Enicocephalomorpha: *Systelloderes*	1	2	1	0	0	–	0	1	0	0	0	0	1	1	0	–	0	0	0	0	1	0	–	0	–	1	0	1	1	1	1	1	1	1	2	1
Dipsocoromorpha: *Cryptostemma*	1	0	1	0	0	–	1	1	0	0	0	0	1	0	0	–	0	0	0	0	1	1	0	1	0	0	–	1	2	1	1	1	1	1	1	2
Dipsocoromorpha: *Hypsipteryx*	1	0	?	?	0	–	0	1	0	0	0	0	1	1	0	–	?	?	?	0	1	0	–	0	–	0	–	1	2	1	?	?	1	?	?	?
Dipsocoromorpha: Schizopteridae	1	–	?	?	0	–	1	1	0	0	0	0	1	0	0	–	?	?	?	0	1	0	–	0	–	0	–	1	2	1	?	?	1	?	?	?
Nepomorpha: *Ochterus*	2	2	1	1	0	–	1	1	0	0	1	1	1	0	0	–	0	0	0	1	1	0	–	0	–	0	–	0	–	0	1	0	1	1	1	1
Nepomorpha: *Corixa*	2	2	1	0	1	1	0	1	0	0	0	0	0	0	0	–	0	0	0	1	1	0	–	0	–	0	–	0	–	0	1	1	?	1	0	?
Nepomorpha: *Gelastocoris*	1	2	1	1	0	–	1	1	1	0	0	1	0	0	0	–	0	0	0	1	1	0	–	0	–	0	–	1	3	0	1	1	1	1	0	1
Nepomorpha: *Lethocerus*	1	0	1	1	0	–	1	1	1	0	1	1	1	0	0	–	0	0	0	1	1	0	–	0	–	0	–	0	–	0	1	1	1	1	2	?
Nepomorpha: *Belostoma*	1	0	1	1	0	–	1	1	0	0	0	1	1	1	0	–	0	0	0	1	1	0	–	0	–	0	–	0	–	0	1	0	1	1	2	2
Nepomorpha: *Hydrocyrius*	1	0	?	?	0	–	0	1	0	0	0	1	1	0	0	–	?	?	?	1	1	0	–	0	–	0	–	0	–	0	1	?	1	1	2	?
Nepomorpha: *Nepa*	1	0	?	?	0	–	0	1	0	0	1	1	1	1	0	–	1	0	0	1	2	0	–	0	–	0	–	0	–	0	?	1	1	1	2	?
Gerromorpha: *Gerris*	1	0	1	1	0	–	0	1	0	0	1	1	1	1	1	0	0	0	0	0	1	0	–	0	–	0	–	1	1	1	1	1	1	1	3	1
Gerromorpha: *Hydrometra*	1	0	0	–	0	–	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	–	1	1	0	–	0	–	1	1	1	1	1	3	–
Leptopodomorpha: *Saldula*	2	2	1	1	0	–	1	1	1	0	0	1	1	0	1	1	1	0	0	0	0	1	0	–	0	–	1	0	1	0	1	0	1	1	1	1	2
Cimicomorpha: *Triatoma*	1	2	1	0	1	0	1	1	0	0	0	0	1	0	0	–	0	0	0	0	0	1	1	1	1	2	1	1	1	1	1	1	1	1	1	0	2
Pentatomomorpha: *Dysdercus*	1	0	0	–	0	–	1	1	0	0	0	–	0	0	0	–	0	0	0	0	0	1	0	–	0	–	0	–	1	0	1	1	1	1	1	0	2

	6 3	7 3	8 3	9 3	0 4	1 4	2 4	3 4	4 4	5 4	6 4	7 4	8 4	9 4	0 5	1 5	2 5	3 5	4 5	5 5	6 5	7 5	8 5	9 5	0 6	1 6	2 6	3 6	4 6	5 6	6 6	7 6	8 6	9 6	0 7
Sternorrhyncha: *Aphis*	2	0	1	1	0	1	0	2	1	0	0	0	1	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	0	0	0	1	0	1	1
Coleorrhyncha: *Hackeriella*	2	0	0	0	0	1	0	2	1	1	0	0	1	0	1	0	1	1	1	1	1	0	1	1	1	0	1	1	1	0	0	1	0	1	1
Enicocephalomorpha: *Systelloderes*	0	0	1	1	0	0	0	2	0	–	1	1	0	0	0	0	2	0	0	0	1	0	0	1	1	0	0	0	1	1	1	1	0	0	1
Dipsocoromorpha: *Cryptostemma*	1	0	1	1	0	0	0	2	0	–	0	1	1	0	0	0	1	0	0	0	1	0	1	1	1	0	0	0	1	0	1	1	0	0	1
Dipsocoromorpha: *Hypsipteryx*	?	0	1	?	?	0	0	2	?	?	?	1	?	?	?	0	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dipsocoromorpha: Schizopteridae	?	0	1	?	?	0	0	–	?	?	0	1	?	?	?	0	1	0	0	0	1	0	1	1	?	?	?	?	?	?	?	?	?	?	?
Nepomorpha: *Ochterus*	2	1	1	1	1	0	1	2	0	–	0	1	1	1	0	1	1	0	0	?	?	?	?	?	1	0	1	0	1	0	1	1	1	1	1
Nepomorpha: *Corixa*	0	0	1	0	1	0	0	1	1	0	0	0	1	1	1	1	1	1	0	0	0	1	0	0	1	0	1	0	1	0	0	0	0	1	1	1	1
Nepomorpha: *Gelastocoris*	1	1	1	1	1	0	1	2	0	–	0	1	1	1	?	1	1	0	1	1	1	0	0	1	1	0	1	0	1	0	1	1	1	1	1
Nepomorpha: *Lethocerus*	?	1	1	0	1	0	1	2	0	–	0	1	1	1	0	1	1	0	0	0	1	1	0	1	1	0	1	0	1	0	0	1	1	1	1
Nepomorpha: *Belostoma*	1	0	1	0	1	0	1	2	1	0	0	1	1	1	0	1	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Nepomorpha: *Hydrocyrius*	?	1	0	0	?	0	1	2	1	0	0	?	?	?	?	?	1	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Nepomorpha: *Nepa*	?	1	1	0	1	0	1	2	1	0	0	1	1	1	0	1	1	0	0	0	1	1	0	1	?	?	?	?	0	?	0	1	?	?	1
Gerromorpha: *Gerris*	2	1	1	0	1	0	1	2	0	–	1	1	1	0	0	1	1	0	0	0	1	1	1	1	1	0	0	0	1	1	1	1	0	0	1
Gerromorpha: *Hydrometra*	2	1	0	0	0	0	0	2	0	–	1	1	0	0	0	1	1	0	0	0	1	0	1	0	1	?	?	?	?	?	?	?	?	?	?	?
Leptopodomorpha: *Saldula*	2	0	1	1	0	0	0	2	0	–	0	1	1	1	0	3	1	1	0	?	?	?	?	?	0	0	0	0	1	0	1	1	1	1	1
Cimicomorpha: *Triatoma*	2	0	0	0	0	0	0	1	1	0	1	1	1	0	0	1	1	1	0	?	?	?	0	?	?	?	?	0	1	0	1	0	1	0	0
Pentatomomorpha: *Dysdercus*	1	0	1	1	1	0	0	1	1	0	0	1	1	0	0	2	2	1	1	0	1	?	0	?	?	?	?	?	0	1	0	0	1	?	?	0

paraphyly of Nepomorpha appear very unlikely. It is apparent that cephalic features alone are insufficient for a clarification of the relationships of the major lineages of Heteroptera. Consequently, we used different published phylogenies to evaluate our set of characters and to discuss different scenarios. In the following the characters are indicated in the text in bold and in parentheses. The numbers correspond to those in Table 2 and Figs. 18 and 19.

Heteroptera is supported as a clade by 12 cephalic apomorphies in our analysis, i.e. the presence of cuticular condyles on the postocciput **(2)** (implying reversal in *Dysdercus*), the presence of a gula **(7)**; the absence of the posterior and anterior tentorial pits (implying reversals in *Saldula*, *Gelastocoris* and *Lethocerus*; homology not fully clarified, see above) **(8**, **9)**; the absence of the tentorium (with possible reversal in the case of the anterior arms of *Nepa* and *Saldula*) **(16**, **17**, **18)**; the origin of the labium on the anterior part of the head capsule **(41)**; the presence of triturating devices (with reduction in several infraorders, see below and COBBEN 1978) **(49)**; the presence of M2a (M. proepisterno-postoccipitalis secundus) **(60)** and the absence of M4 (depressor of the head, connecting the pronotum and the posterior tentorial arms) **(61)** and M11 (loral apodeme-postclypeal muscle) **(63)**.

Hypotheses based on different data sets were presented by MAHNER (1993), WHEELER et al. (1993), SHCHERBAKOV & POPOV (2002), XIE et al. (2008), and LI et al. (2012b). We mapped our character data on three al-

List of characters

0 orientation of base of mouthparts relative to head: (0) posteriorly or posteroventrally = hypognathous; (1) anteriorly = prognathous; (2) ventrally = orthognathous
1 number of ocelli: (0) 0; (1) 3; (2) 2
2 cuticular condyles of postocciput: (0) absent; (1) present
3 shape and number of postoccipital condlyes: (0) 2 processes; (1) 2 short + 2 long processes
4 subdivision of clypeus: (0) absent; (1) present
5 classification of clypeal subdivision: (0) subdivided in ante- and postclypeus; (1) additional paraclypeus
6 bucculae: (0) absent; (1) present
7 gula: (0) absent; (1) present
8 anterior tentorial pits: (0) absent; (1) present
9 posterior tentorial pits: (0) absent; (1) present
10 epicranial (=coronal) suture (adults): (0) absent; (1) present
11 frontal suture (adults): (0) absent; (1) present
12 epistomal ridge (separates clypeus from frons): (0) absent; (1) present
13 genal suture (separates lorum from remainder of head capsule): (0) absent; (1) present
14 pairs of cephalic trichobothria: (0) absent; (1) present
15 origin of cephalic trichobothria: (0) in a deep pitlike depression; (1) in a flat depression
16 anterior tentorial arms: (0) absent; (1) present
17 posterior tentorial arms: (0) absent; (1) present
18 corpotentorium: (0) absent; (1) present
19 antenna folded under head, received in a groove formed by genae: (0) absent; (1) present
20 number of antennomeres of flagellum: (0) 5 or more; (1) 4; (2) 3
21 basiflagellite equipped with R-Structure (Zrzavý 1990): (0) absent; (1) present
22 type of R-Structure of basiflagellite (Zrzavý 1990): (0) Bf(RVI); (1) Bf(RI)
23 distiflagellite equipped with R-Structure (Zrzavý 1990): (0) absent; (1) present
24 type of R-Structure of distiflagellite (Zrzavý 1990): (0) Df(RVI); (1) Df(RV); (2) Df(RI)
25 intercalary slerite between scapus and pedicellus ("prepedicellite, pp") (Zrzavý 1990): (0) absent; (1) present
26 types of prepedicellite (Zrzavý 1990): (0) pp(I); (1) pp(II)
27 intercalary sclerite ("preflagelloid, pf" or "prebasiflagellite, pb") between antennomeres 2 and 3 (Zrzavý 1990): (0) absent; (1) present
28 type of preflagelloid or prebasiflagellite (Zrzavý 1990): (0) pf(I); (1) pf(II); (2) (pfIV); (3) pb
29 intercalary sclerite ("intraflagelloid, if") between antennomeres 3 and 4 (Zrzavý 1990): (0) absent; (1) present as if(I)
30 origin of extrinsic antennal muscles (M6, M. depressor scapi + M7, M . levator scapi): (0) anterior armstentorium; (1) head capsule;
31 protrusion of the proximal mandibular part in a long and slender apodeme or tendon: (0) absent; (1) present
32 shape of mandibular stylets in lateral view: (0) linear; (1) boomerang-shaped
33 mandibular lever ("Protraktorarm" of Weber 1928): (0) absent; (1) present
34 shape of mandibular lever (characters 0–2 from Rieger 1976): (0) equilateral triangle; (1) acute triangle, arm attached to mandible elongated; (2) acute triangle, arm attached to mandible elongated directed caudally; (3) quadrangular; (4) bar-shaped
35 formation of salivary canal: (0) by indentation of right maxilla; (1) by indentation of left maxilla; (2) mutual or variable in entire labial length
36 shape of maxillary stylets in cross-sectional view: (0) compressed dorso-ventrally; (1) compressed laterally; (2) circular
37 setae at tip of maxilla: (0) absent; (1) present
38 barb-like structures at tip of maxilla: (0) absent; (1) present
39 maxillary lever: (0) absent; (1) present
40 maxillary glands ("cephalic glands"): (0) absent; (1) present
41 origin of labium: (0) anterior part of head capsule; (1) cervical region
42 intercalary sclerites between 3rd and 4th labial segment (1 pair): (0) absent; (1) present
43 number of labial segments: (0) 1; (1) 3; (2) 4
44 sensilla at apex of labial rostrum: (0) absent; (1) present
45 sensilla grouping: (0) one group; (1) two rows
46 interlocking of the edges of the labial groove: (0) absent; (1) present
47 orientation of hypopharynx (including pumping chamber): (0) dorso-ventral; (1) cranio-caudal
48 origin of retractor muscle of piston (M23, M. retractor pistilli): (0) posterior region of head capsule; (1) hypopharyngeal wing
49 pharyngeal triturating devices ("striated plates"; "Kauapparat"): (0) absent; (1) present
50 distinct bent (dorso-ventral orientation to cranio-caudal) of pharynx: (0) absent; (1) present
51 principal salivary gland: (0) obscurely bi-lobed; (1) distinctly bi-lobed; (2) four-lobed; (3) single-lobed
52 structure of accessory gland: (0) vesicular; (1) tubular
53 structure of principal gland: (0) aciniform; (1) irregular
54 length of principal duct: (0) short; (1) long
55 triangular processes of tritocerebrum: (0) absent; (1) present
56 fusion of subesophageal ganglion with brain (to dts): (0) absent; (1) present
57 fusion of subesophagealganglion or dts with first thoracic ganglion: (0) absent; (1) present
58 frontal ganglion: (0) distinct; (1) indistinct, reduced in size
59 circumesophageal connectives: (0) elongate; (1) short and broad
60 M2a (M. proepisterno-postoccipitalis secundus): (0) absent; (1) present
61 M4 (depressor of the head, connecting the pronotum and the posterior tentorial arms): (0) absent; (1) present
62 M5a (M. dilatator oris glandulae capitis): (0) absent; (1) present
63 M11 (loral apodeme-postclypeal muscle): (0) absent; (1) present
64 M12a (M. retractor setae mandibularis secundus): (0) absent; (1) present
65 M12b (M. retractor setae mandibularis tertius): (0) absent; (1) present
66 M14 (M. protractor setae mandibularis secundus): (0) absent; (1) present
67 M20a (M. transversalis labii secundus): (0) absent; (1) present
68 M28 (M. dilatator postpharyngis dorsalis): (0) absent; (1) present
69 M29 (M. dilatator postpharyngis ventralis): (0) absent; (1) present
70 M19 (M. transversalis labii primus): (0) absent; (1) present

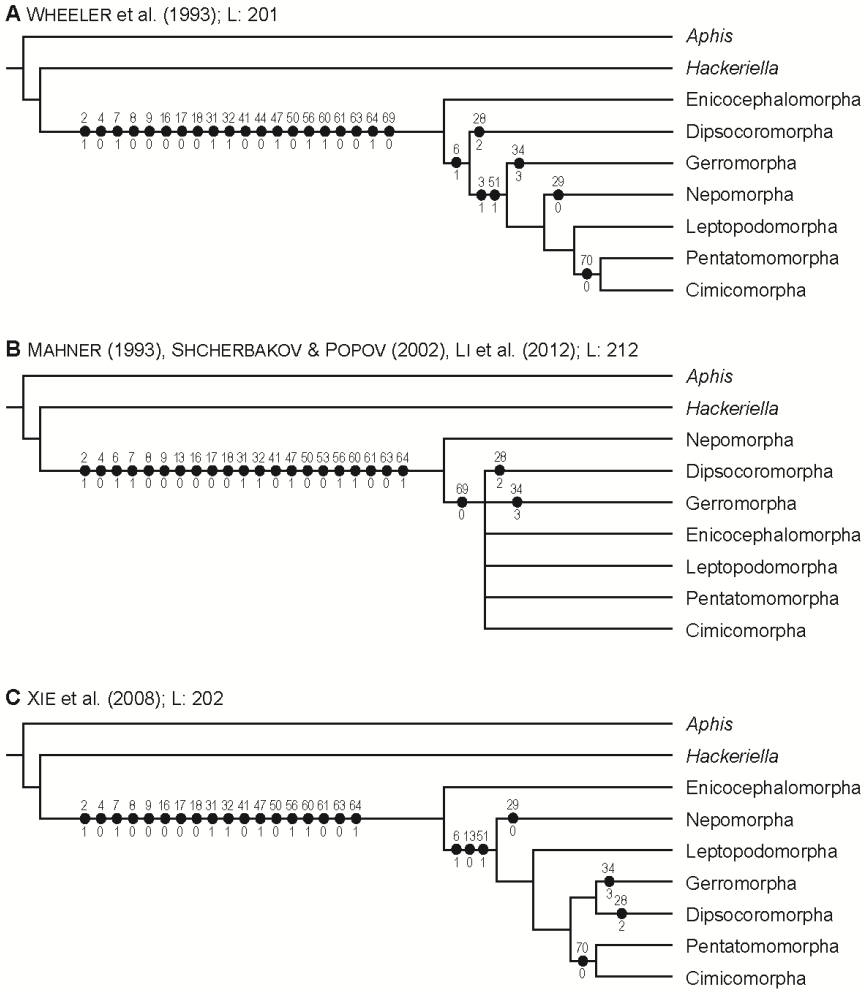

Fig. 19. **A**: phylogeny after WHEELER et al. (1993) (modified); **B**: phylogeny after MAHNER (1993), SHCHERBAKOV & POPOV (2002) and LI et al. (2012b) (modified); **C**: phylogeny after XIE et al. (modified). Full circles show unambiguous apomorphic character states, white circles for homoplasious changes not shown. The numbers correspond to those in chapter 4 and Table 2.

ternative topologies using Winclada (Fig. 19). The most parsimonious hypothesis is that of WHEELER et al. (1993, fig. 5), which required 201 steps (Fig. 19A), whereas 202 and 212 were required under the phylogenies suggested by XIE et al. (2008) (Fig. 19C) and MAHNER (1993) (Fig. 19B), respectively. The monophyly of Heteroptera is supported in the case of WHEELER et al. (1993) by 20 cephalic autapomorphies (Fig. 19A), in the case of MAHNER (1993) by 21 (Fig. 19B), and in the scenario of XIE et al. (2008) by 18 (Fig. 19C). In contrast, there are only single or very few apomorphies supporting major infraordinal branches, i.e. those supporting relationship between the infraorders. In the tree of WHEELER et al. (1993) (Fig. 19A), Euheteroptera (Heteroptera excl. Enicocephalomorpha) are supported by the presence of distinct bucculae **(6)**, monophyletic Dipsocoromorpha by the presence of the preflagelloid antennal type IV **(28)**, Neoheteroptera (Euheteroptera excl. Dipsocoromorpha) by the presence of paired cuticular condyles of the postocciput **(3)** and distinctly bi-lobed principal glands **(51)** (Fig. 19A), and Gerromorpha by the presence of cephalic trichobothria originating in a deep pit-like depression (**15**, not displayed in Fig. 19A) and a quadrangular mandibular lever **(34)**. No cephalic features support Panheteroptera (Neoheteroptera excl. Gerromorpha) (Fig. 19A). Nepomorpha is supported by the absence of the intraflagelloid between

Table 3. List of taxa and corresponding literature used for morphological comparison and phylogenetic reconstruction.

Taxa	Literature
Dipsocoromorpha	
Hypsipteryx sp. (Dipsocoridae)	Štys 1970
Schizopteridae	Emsley 1969
Nepomorpha	
Ochterus marginatus (Latreille, 1804) (Ochteridae)	Rieger 1976
Corixa punctata (Illiger, 1807) (Corixidae)	Benwitz 1956
Gelastocoris oculatus (Fabricius, 1798) (Gelastocoridae)	Parsons 1958, 1959, 1960a,b
Lethocerus uhleri (Montandon, 1896) (Belostomatidae)	Parsons 1968
Belostoma sp. (Belostomatidae)	Verma et al. 1973; Swart & Felgenhauer 2003
Hydrocyrius columbiae columbiae Spinola (Belostomatidae)	Kopelke 1978
Nepa cinerea Linnaeus, 1758 (Nepidae)	Hamilton 1931; Rieger 1976
Gerromorpha	
Gerris sp. (Gerridae)	Matsuda 1960; Cranston & Sprague 1961; Andersen 1982
Hydrometra martini Kirkaldy, 1900 (Hydrometridae)	Sprague 1956; Andersen 1982
Leptopodomorpha	
Saldula pallipes (Fabricius, 1794) (Saldidae)	Parsons 1962, 1963
Cimicomorpha	
Triatoma infestans Klug, 1834 (Reduviidae)	Barth 1952a,b, 1953a,b; Rieger 1976
Pentatomomorpha	
Dysdercus koenigii Fabricius (Pyrrhocoridae)	Kumari 1955
Dysdercus fasciatus Signoret (Pyrrhocoridae)	Khan 1972
Outgroups	
Aphis fabae Scopoli, 1763 (Sternorrhyncha, Aphididae)	Weber 1928, 1929; Forbes 1977
Hackeriella veitchi (Hacker, 1932) (Coleorrhyncha, Peloridiidae)	Spangenberg et al. 2013

antennomeres three and four **(29)**. A potential additional nepomorphan autapomorphy is the position of the antenna that is folded underneath the head, but a very similar condition is present in Coleorrhyncha, arguably a result of parallel evolution. A potential synapomorphy of Pentatomomorpha and Cimicomorpha is the absence of M19 (M. transversalis labii primus) **(70)** (Fig. 19A).

In Mahner (1993), Nepomorpha are placed as the sister group of the remaining Heteroptera. A potential apomorphy of Heteroptera excluding Nepomorpha is the reduction of M29 (M. dilatator postpharyngis ventralis) **(69)** (Fig. 19B). This scenario appears less likely considering the number of steps and the implied character transformations.

Xie et al. (2008) suggested the monophyly of Euheteroptera as in Wheeler et al. (1993), but with Nepomorpha, instead of the Dipsocoromorpha, in a second basal position (Fig. 19C). Euheteroptera was supported by three potential apomorphies: the presence of distinct bucculae **(6)** (in agreement with the hypothesis of Wheeler et al. 1993), a reduced genal suture **(13)**, and distinctly bi-lobed principal salivary glands **(51)**.

Even though parsimony favors the pattern of Wheeler et al. (1993), with basal Enicocephalomorpha, and Dipsocoromorpha as the second branch, it is apparent that this issue is far from being settled. Apparently, morphological characters of the head are not sufficient for a reliable reconstruction of phylogenetic relationships of the major heteropteran lineages. The hemipteran head is highly derived, but main features are conserved within the entire lineage and within the megadiverse Heteroptera. This is likely linked to the ubiquitous mechanism of liquid feeding and related functional constraints. Predacious feeding habits are presumably an apomorphic groundplan feature of Heteroptera and this has resulted in an entire series of cephalic character transformations, among them prognathism and the related presence of a gula and modified insertion of the labium (Sweet 1979). The ancestral feeding habits were largely maintained in the basal lineages, again resulting in more or less conserved cephalic structures. Evolutionary changes of cephalic features related with a switch to phytophagy may have played a role in the evolution of some of the "higher" heteropteran groups, i.e. the Pentatomomorpha and Cimicomorpha. An evaluation of this hypothesis is currently impeded by a severe lack of detailed morphological data.

What is apparently needed for a reliable phylogenetic reconstruction is more detailed morphological data, not only covering the head structures of a broader taxon sampling, but also features of the thorax and abdomen including the genitalia. This approach combined with extensive molecular data assembled in the 1KITE project (http://www.1kite.org/) and the hemipteroid AToL project (http://www.nsf.gov/awardsearch/showAward?AWD_ID=1239788&HistoricalAwards= false) will likely lead to a robust heteropteran phylogeny, which will be an ideal basis for developing a complex evolutionary scenario using well documented morphological (and palaeontological) information.

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3.2 New nomenclature especially for hemipteran musculature or muscles not present in Friedrich & Beutel (2008) or Wipfler et al. (2011)

Table 2: Musculature not dealt with in Friedrich & Beutel (2008) and Wipfler et al. (2011). An additional nomenclature is introduced for either evolutionary speaking new muscles or derivatives of present musculature. The separation, however, is not apparent.

	origin	insertion	function
0anx1 (likely an antagonistic bundle of 0an8)	lateral base of pedicellus	lateral base of 1st flagellomere	flexor of flagellum
0lbx1 (lm of *Macroxyela*)	longitudinal muscle of epipharynx		
0lbx2 (35. of Mickoleit 1963) likely homologous to 0lb3. The latter, however, extends from the epistomal sulcus to the basal labral wall.	right rudiment of anterior tentorial arm	dorsal epipharynx	
0mdx1 (M12a of Spangenberg et al. 2013b), likely homologous to 0md1, 0md2 or 0md3	postocciput	proximally on mandibular tendon	retractor
0mdx2 (M12 of Spangenberg et al. 2013a,b), likely homologous to 0md1, 0md2 or 0md3	genal region	mesal part of mandible	retractor
0mdx3 (M14 of Spangenberg et al. 2013b). The lateral position of the mandibular lever and the occurrence of the fusion with the mandibular body resemble the structure of the mandibular abductor tendon. Thus, the homology of the hemipteran mandibular protractors with 0md2 or 0md3 appears also likely.	dorsally on roof of head capsule, anterad compound eyes	laterally on mandibular lever	protractor
0mdx4 (M13 of Spangenberg et al. 2013b). The lateral position of the mandibular lever and the occurrence of fusion with the mandibular body resemble the structure of the mandibular abductor tendon. Thus, the homology of the hemipteran mandibular protractors with 0md2 or 0md3 appears also likely.	border region of head capsule/ clypeus	laterally on mandibular lever	protractor
0mdx5 (“8” of Arora & Singh 1962). The lateral position of the mandibular lever and the occurrence of fusion with the mandibular body	dorsally on posterior margin of lorum	mesal side of mandibular stylet	protractor

resemble the structure of the mandibular abductor tendon. Thus, the homology of the hemipteran mandibular protractors with 0md2 or 0md3 appears also likely			
0mdx6 (8 of Singh 1971) (clearly separated from preceding mandibular retractors, likely homologous to 0md1, 0md2 or 0md3)	cranium	mandibular base	retractor
0mdx7 (10 of Rilling 1960) (Homology impeded as there is apparently no mandibular muscle with posttentorial origin in an generalized insect)	posterior tentorial arm	mandibular base	retractor
0mxx1 (“maxillary muscle”), likely a separated bundle of 0mx2	lateral head capsule or gena, separated from 0mx2	base of lacinia	retractor
0mxx2 (13. of Haub 1967; second muscle located between 2nd and 4th maxillary palpomere)	2nd maxillary palpomere	border region of 3rd and 4th maxillary palpomere	levator of apical palpomeres
0mxx3 (14. of Mickoleit 1963, retractor of maxillary lever), likely a separated bundle of 0mx2	cranium or tentorium	maxillary lever/Artikulationshebel	retractor
0mxx4 (10. M. lacinio-mandibularis of Mickoleit 1963)	base of maxillary lever	base of mandible or mandibular pouch	fixation of mandible
0mxx5 (protractor of lacinia via maxillary lever, pmxl), homology to a separated partition of 0mx6 uncertain	stipes or maxillary plate, respectively	maxillary lever	protractor
0mxx6 (M. tentorio-lacinialis, m.retr.max1 of Weber 1935). Either a separated partition of 0mx2 with the origin shifted from the cranium to the tentorium, or a part of 0mx3 with the insertion shifted from the cardo to the lacinia, or a part of 0mx4 or 0mx5 with the insertion shifted from the stipes to the lacinia,or a complete separated muscle.	corpotentorium	proximal side of laciniae	retractor
0mxx7 (muscle of maxillary gland)	hypopharyngeal wing or posterad to that	maxillary gland	
0mxx8 (2nd muscle of 1st maxillary palpomere) (M43 of Staniczek	base of palpomere 1	base of palpomere 2	depressor of dis-

2001). (Wipfler et al. [2011] homologized both Staniczeks' M42 and M43 with 0mx12. The homology proposed in this study disagrees with this approach as M42 and M43 are distinctly distinguished by different origins [M42 laterally on base of palpomere 1, M43 medially on base of palpmore 1] and insertions sides [M42 laterally on base of palpomere 2, M43 medially on base of palpomere 2]. As a consequence, M42 acts as levator and M43 as depressor of the distal palpomeres, which appears unlikely in the functionality of a single muscle.)			tal palpomeres
0mxx9 (g.m.f. of Noland 1924)	anterad origin of 0mx7	proximal knob of galea	antagonist towards 0mx7, flexor of galea
0lax1 (m. abd2 of Weber 1928, M19) likely homologous to 0la5 or 0la6 depending each on the homology of the single labial segments	proximal edge of 1st labial segment	distal edge of 1st labial segment	abductor
0lax2 (m. add1 of Weber 1928, M17a)	distal region of 1st labial segment	border region of 1st and 2nd labial segment	adductor
0lax3 (m. add2 of Weber 1928, M18)	lateral side of 1st labial segment	lateral border region of 1st and 2nd labial segment	adductor
0lax4 (m. add3 of Weber 1928, M20)	distal border region of 1st and 2nd labial segment	distal edge of 3rd labial segment	adductor
0lax5 (m. add4 of Weber 1928)	lateral proximal edge of 2nd labial segment	distal edge of 3rd labial segment	adductor
0lax6 (m. add5 of Weber 1928)	labial groove	lateral distal edge of 3rd labial segment	adductor
0lax7 (m. abd3 of Weber 1928, M22)	laterobasal margin of 3rd labial segment	proximal edge of 4th labial segment	abductor of terminal segment

0lax8 (m. trans1 of Weber 1928)	lateral wall of 2nd labial segment	labial groove	extension of labial groove
0lax9 (m. trans.2–4 of Weber 1928, M20a),	lateral wall of 3rd labial segment	labial groove	extension of labial groove
0lax10 (m. trans5 of Weber 1928, M21)	proximal lateral wall of 3rd labial segment	distal region of labial groove in 3rd labial segment	extension of labial groove
0lax11 (21 of Singh 1971, muscle of crumena)	pronotum	crumenal mouth	retractor?
0lax12 (22 of Singh 1971, muscle of crumena)	basal labial segment	crumenal mouth	depressor?
0lax13 (16 of Singh 1971)	mesosternum	base of labium	
0lax14 (M17, likely homologous to 0la5 or 0la6)	posterior tentorium or cranium	first labial segment	levator of labium
0lax15 (H3A of Parsons 1968)	laterally on suspensory plate	dorsal wall of oblique plate between 1st and 2nd labial segment	
0lax16 (36 of Rilling 1960)	transversal muscle of 4th labial segment		
0lax17 (Oism of Weber 1928)	protergit	caudal edge of 1st labial segment	
0lax18 (28 of Singh 1971)	transversal muscle at distal end of 3rd labial segment		
0lax19 (19 of Singh 1971)	mesonotum	labium	
0lax20 (20 of Singh 1971)	gena	2nd labial segment	
0lax21 (M52 of Stanizcek 2001) (Due to the insertion and the additional presence of M51 with mediobasal insertion, M52 is not considered as homologous with 0la16 as proposed by Wipfler et al. 2011.)	laterobasal end of 1st labial palpomere	laterobasal end of 2nd labial palpomere	
0lax22 (M53 of Staniczek 2001) (Due to the insertion and the additional presence of M51 with mediobasal insertion, M53 is not	anterior edge of 1st labial palpomere	anterior basal margin of 2nd labial segment	

considered as homologous with 0la16 as proposed by Wipfler et al. 2011.)			
0lax23 (27 of Singh 1971)	dorsolateral walls of the third labial segment	base of the labial groove laterally	
0hyx1 (h of Badonnel 1934)	apodeme of ovoidal sclerite (hypopharynx)	prementum	protractor of hypopharynx
0hyx2 (Tentorialligament, ligament fibreux of Badonnel 1934)	corpotentorium	posterior region of cibarial sclerite	
0hyx3 (46 of Singh 1971)	anteriolateral region of pronotum	hypopharyngeal wing	
0hyx4 (M24 of Spangenberg et al. 2013a) (likely a separated bundle of 0hy12)	hypopharyngeal wing	fused principal salivary ducts	
0hyx5 (m. retr. pist1 of Weber 1928) (likely a separated bundle of 0hy12)	posterior region of hypoharynx, close to corpotentorium	anterior region of piston	retractor of piston
0hyx6 (m. dil. cup2 of Weber 1928), homology to 0hy12 impeded by numerous different origins of m. dil. cups	posterior wall of hypopharynx	posterior region of salivary pumping chamber	dilator of pumping chamber
0hyx7 (m. dil. cup3 + 4 of Weber 1928) homology to 0hy12 impeded by numerous different origins of m. dil. cups	anterior region or hypopharynx	anterior region of salivary pumping chamber	dilator of pumping chamber
0hyx8 (m. dil. cup5 of Weber 1928) homology to 0hy12 impeded by numerous different origins of m. dil. cups	lateral wall of hypopharynx	lateral wall of salivary pumping chamber	dilator of pumping chamber
0hyx9 (Msusph of Beutel et al. 2010)	suspensorial tendon/oral hypopharyngeal arm	dorsal wall of anatomical mouth opening	
0hyx10 (30. of Mickoleit 1963)	muscle connecting both afferent salivary ducts		
0hyx11 (7. of Weber 1969)	longitudinal muscle of wall of salivarium		
0hyx12 (36 of Khattar 1964), likely a separated bundle of 0hy12	base of "distal lateral sclerite of hypopharynx	tip of the salivos just behind the opening of the common salivary duct	

0bux1 (1st pair of Snodgrass 1927) likely homologous to 0bu3 or a separated bundle of 0bu2	anterior frons	dorsal pharynx	dilator
0phx1 (M. sitophori pharyngis)	oral hypopharyngeal arm	ventral pharynx	dilator
Idx1 (43 of Weber 1969)	transversal muscle between both lateral cervical sclerites		
Idx2 (Mxy of Beutel & Weide 2005)	transversal muscle of the vertex		
Ivlmx1 (Ovlm1 of Weber 1928)	proepisternum	laterad edge of head	
Ivlmx2 (No. 19 of Chisholm 1962)	apophysis of mesosternum	posterior tentorial arms	
Idvmx1 (M4) 44 of Singh	pronotum	posterior tentorial arm	
Idvmx2 (49 of Singh 1971)	prothorax	gena	
Idvmx3 (M2a), similar in position to Ipcm1, however the latter originates from the procoxa whereas it is the anterior edge of the prosternum in Hemiptera	anterior region of proepisternum	dorsal postocciput	levator or rotator
Idvmx4 (m. tent1 of Weber 1928, other than Idvmx1)	epicranium	corpotentorium	
Idvmx5 (41, 42, 63 of Weber 1969)	sternum	lateral cervical sclerite	
Ipcmx1 (46 of Weber 1969)	trochanter 2	lateral cervical sclerite	
Ipcmx2 (50 of Weber 1969)	coxa 2	lateral cervical sclerite	
Ipcmx3 (51 of Weber 1969)	coxa 3	lateral cervical sclerite	
Ipcmx4 (38 of Weber 1969)	propleura	lateral cervical sclerite	

3.3 List of characters included in the matrix

0 orientation of base of mouthparts: (0) hypognathous (posteriorly or posteroventrally); (1) prognathous (anteriorly); (2) orthognathous (ventrally)

1 exposure of head capsule: (0) fully exposed, not retracted into prothorax; (1) partly retracted into prothorax

2 head shape in dorsal view: (0) not triangular, without caudally tapering posterior part; (1) triangular with caudally tapering posterior part

4 symmetry of head: (0) symmetrical; (1) asymmetrical (right mandible reduced, asymmetrical anteclypeus, clypeoloral cleft only present on left side)

5 head shape in lateral view: (0) not flattened dorso-ventrally; (1) dorso-ventrally flattened (e.g. Figs. 17B, 19B). The dorso-ventrally flattened head (and body) is apparently an adaptation to the ectoparasitic life style in Phthiraptera.

6 shape of anterior cephalic region compared to posterior part: (0) not distinctly flattened dorso-ventrally; (1) dorso-ventrally flattened

7 sclerotization of head capsule: (0) complete, vertex, frons and genae sclerotized; (1) incomplete, vertex, frons and genae membranous

8 areolae, thin cephalic fenestrations: (0) absent; (1) present

9 surface structure of genal rim: (0) glabrous; (1) equipped with thorns and sensilla; (2) equipped with long sensilla in a comb-like configuration; (3) equipped with irregularly distributed setae

10 first pair of lateral cervical sclerites (articulation with head capsule): (0) absent; (1) present

11 second pair of lateral cervical sclerites (articulation with episternum): (0) absent; (1) present

12 dorsal cervical sclerite(s): (0) absent; (1) present

13 dorsal cervical sclerite(s): (0) paired; (1) unpaired

18 ocelli: (0) absent; (1) present. Species of Schizopteridae are either equipped with two ocelli or ocelli are absent (Emsley 1969).

19 number of ocelli: (0) 3; (1) 2

20 ocellar elevation ("Ocellenhügel"; Mickoleit 1963): (0) absent; (1) present

21 ocular point ("Augenhügel"; Tröster 1990a), (op) (Fig. 27B) (Stojanovich 1945), sclerotized hook posterad antennal articulation: (0) absent; (1) present

23 division of compound eye into two subunits: (0) incomplete or absent; (1) present

24 number of the ommatidia: (0) 7 to 8 (Fig. 17B) (see also Yang et al. 2012); (1) more than 8; (2) 2 (Fig. 19B). The lateral eye of "Mallophaga" with its single lens is a reduced compound eye and called “pseudocellus” (Wundrig 1936); (3) 1

28 cone-shaped protrusions of frons ("Frontalkegel" of Weber 1929a; "genal lobe" of Singh 1971): (0) absent; (1) present.

29 longitudinal ridges on frons (carinae): (0) absent; (1) present

30 dorsal shift of foramen occipitale: (0) absent; (1) present, dorsal; (2) semi-dorsal

31 size of foramen occipitale: (0) pantotrem, constriction between prothorax and head capsule indistinct; (1) mesotrem, narrow foramen (in some cases shifted ventrad)

32 condyles of postocciput: (0) absent; (1) present. “Occipital condylar facet” of *Idiocerus* (Arora & Singh 1971); “Kehlsporn” of Thysanoptera (Mickoleit 1963); “occipital apophysis” of *Haematopinus* (Stojanovich 1945); “Occipitalapophysen” of *Hybophthirus* (Tröster 1990a).

33 shape and number of condyles: (0) 2 processes dorsally; (1) 2 ventral + 2 dorsal processes (likely fused each to an unpaired apodeme); (2) 2 processes ventrally ("Kehlsporn" of Mickoleit 1963) to laterally

34 subdivision of clypeus (by suture or by different structural properties of two areas): (0) absent; (1) present

35 clypeal subdivisions: (0) ante- and postclypeus (both not enlarged); (1) as (0) + additional paraclypeus; (2) small anteclypeus and distinctly enlarged bulbous postclypeus (with striped pattern in Cicada); (3) small strip-like anteclypeus and moderately swollen postclypeus (in comparison to Cicadomorpha)

36 anteclypeus or anterior region of clypeus: (0) sclerotized; (1) membranous

37 clypeal suture, "Clypealnaht" (Mickoleit 1963) (separates anteclypeus from postclypeus): (0) absent; (1) present.

38 paired clypeal arms ventrally partly enclosing labrum, each bearing a cone (Tröster 1990a) (cc1) (Figs. 27C,D): (0) absent; (1) present

40 bucculae: (0) absent; (1) present

41 gula (gu) (e.g. Figs. 17C, 19C, 21C): (0) absent; (1) present. “posterior plate” of *Lethocerus* (Parsons 1968); “hypostomal bridge” of *Belostoma* (Verma et al. 1973); “hypostomal bridge” of *Dysdercus* (Kumari 1955; Khan 1972)

42 mandibular plates (lora): (0) absent; (1) present. Lateral piece of clypeus (“Seitenteil des Clypeus”) of *Ochterus* (Rieger 1976); “paraclypeus“ of *Dysdercus* (Kumari 1955)

43 structure of mandibular plates: (0) membranous, indistinct; (1) sclerotized, distinct (Weber 1929)

44 anterior tentorial pits: (0) absent; (1) present. “anterior grooves” of *Zorotypus* (Beutel & Weide 2005); pits where the "clypeal connectives" of *Gelastocoris* are attached (Parsons 1959); “distinct indentions” of *Saldula* (Parsons 1962); “grubenförmige Spuren der Einstülpungen” of *Trimenopon* (Stöwe 1943). Neither anterior nor posterior tentorial pits were depicted in illustrations of *Lepyronia* (Kramer 1950). As both structures are

minute but present in other cercopid species (i.a. *Ptyelus nebulosus* (LETHIERRY, 1876) in Singh [1971]) it is likely that they are also present in *Lepyronia*.

45 posterior tentorial pits: (0) absent; (1) present. “langgezogene Einstülpungen” of *Myrsidea* (Buckup 1959); “Tentoriumspuren“ of *Haematomyzus* (Weber 1969).

46 epicranial (=coronal) suture (adults): (0) absent; (1) present. “Y-förmige Häutungsnaht” of *Hybophthirus* (Tröster 1990a).

47 frontal suture (adults) (frs) (e.g. Figs. 17A, 21A): (0) absent; (1) present. “frontal suture” + “frontogenal suture” of *Schizodactylus* (Khattar 1958); “U-shaped indention” of *Gelastocoris* (Parsons 1959); the frontal suture of *Platypleura* is not labelled but depicted in fig. 1 of Singh (1971) (compare also with fig. 19 of Kramer [1950]); “epicranial suture” of *Belostoma* (Vermal et al. 1973); “postfrontal suture” of *Psocus* (Cope 1940): “Clypeo-Frontalleiste” of *Trochiloecetes* (Haub 1983); “Clypeo-Frontalleisten” of *Bovicola* (Risler 1951); “Clypeofrontalleisten” of *Ornithobius* (Haub 1971); “Epistomalleisten” of *Hybopthirus* (Tröster 1990a)

48 epistomal ridge (separates clypeus from frons): (0) absent (=clypeofrons); (1) present. transverse groove between ante- and postclypeus (the latter is the frons *sensu stricto*) of *Lethocerus* (Parsons 1968); “postclypeus groove” of Belostoma (Verma et al. 1973); “frontal suture” of *Nepa* (Hamilton 1931)

50 pulvinus (pv) (Figs. 17C, 22B) (e.g. Symmons 1952, Smith 2001) or “Pulvinarien” (Haub 1983) as "enlarged clypeo-labral suture forming a thick unsclerotized pad that serves to support the feather or hair shaft during attachment or feeding" (Smith 2001): (0) absent; (1) present

54 clypeoloral cleft (separates lorum/mxpl from clypeus) or clypeo-genal-ridge: (0) absent; (1) present. As shown in fig. 2B of Spangenberg et al. (2013b) (*Systelloderes*, Enicocephalidae, Heteroptera) the cylpeoloral cleft continues anterad to separate the clypeus from the gena. Thus, it resembles the clypeo-genal ridge of *Osmylus* (Beutel et al. 2010); “frontogenal suture” of *Schizodactylus* (Khattar (958); “clypeal fold” of Schizopteridae (Emsley 1969); “lateral clypeus groove” of *Belostoma* (Vermal et al. 1973); “clypeal groove” of *Dysdercus* (Kumari 1955; Khan 1972). Not applicable for *Gelastocoris* (Parsons 1959) and *Melicharia* (Singh 1971) as the lora are partly fused with the clypeus.

55 symmetry of clypeoloral cleft/Clypeo-Genal-Naht: (0) symmetrical; (1) fully developed on left side, vestigial on right side

56 genal suture (separates lorum from rest of head capsule): (0) absent; (1) present

57 "Wangenspalt" (Mickoleit 1963) as lateral cleft in head capsule extending from margin of postocciput to gena: (0) absent; (1) present

58 "ventrale Längsleisten" (vL) (Fig. 22G), (Risler 1951) enclosing labium and gula: (0) absent; (1) present. “Occipitalleisten” of *Ornithobius* (Haub 1971) and *Hybophthirus* (Tröster 1990a).

59 pleurostomal ridge (connecting both mandibular jaws, Risler 1951): (0) absent; (1) present

60 cephalic trichobothria: (0) absent; (1) present

63 position of point C (articulation point of mandibular lever with head capsule or dorsal end of loromaxillary cleft separating maxillary plate from lorum) (Parsons 1974): (0) near level of anterior tentorial pits or compound eyes; (1) below level of anterior tentorial pits or compound eyes, shifted to anterior region of head capsule

64 ventromedian rim between mandibles and anterior cephalic margin (for fixing hairs or feathers) (Mey 2005): (0) absent; (1) present

65 mixing of food with saliva: (0) after ingestion; (1) before ingestion (Puchkova 1970; see also von Kéler 1966b)

66 salivary meatus, "Speichelhöhle" (between labium, hypopharynx, maxillae and mandibles) (von Kéler 1966a), see also fig. 20.3 in Mey 2005: (0) elements incompletely united, laterally open; (1) completely united, mandibles and maxillae fused with labium ("Stachelhöhle") (e.g. Mey 2005)

67 meatus oris (closed cavity delimited by mandible mesally, labium ventrally, and clypeolabrum laterally) (see fig 20.3 of Mey 2005): (0) absent; (1) present

69 Idlm1, M. prophragma-occipitalis: (0) absent; (1) present

70 Idlm2, M. pronoto-occipitalis: (0) absent; (1) present

71 Idlm3, M. prophragma-cervicalis: (0) absent; (1) present

73 Idvm1, M. cervico-occipitalis anterior: (0) absent; (1) present

76 Idvm4, M. pronoto-cervicalis lateralis: (0) absent; (1) present

77 Idvm5, M. pronoto-cervicalis anterior: (0) absent; (1) present

78 Idvm6, M. pronoto-cervicalis medialis: (0) absent; (1) present

79 Idvm9, M. profurca-occipitalis: (0) absent; (1) present

80 Idvmx1, “M. pronoto-tentorialis primus”: (0) absent; (1) present

81 Idvmx2, “M. pronoto-genalis”: (0) absent; (1) present

82 Idvmx3, “M. proepisterno-occipitalis”: (0) absent; (1) present

83 Idvmx4, “M. pronoto-tentorialis secundus”: (0) absent; (1) present

84 insertion of Idvm4, M. pronoto-cervicalis lateralis: (0) postocciput; (1) posterior tentorial arm; (2) apodeme of maxillary plate; (3) postocciput + posterior tentorial arm; (4) lateral cervical sclerite. According to Friedrich & Beutel (2008) the muscle Idvm4 is highly variable in origin and insertion.

86 Itpm1, M. pleurocrista-occipitalis: (0) absent; (1) present

88 Ipcm1, M. procoxa-cervicalis: (0) absent; (1) present

89 Ipcm2, M. procoxa-cervicalis transversalis: (0) absent; (1) present

94 Ivlm1, M. profurca-cervicalis: (0) absent; (1) present

96 Ivlm3, M. profurca-tentorialis: (0) absent; (1) present

97 Ivlmx1: (0) absent; (1) present

101 Lig3 of Tröster (1990a), from ventral side of head capsule to dorsal head capsule, below antennal articulation: (0) absent; (1) present. For *Haematopinus* see Tröster (1990a, p. 20).

102 Lig4 of Tröster (1990a), from lateral edges of ventral pre-oral cavity to hypostomal ridge, connected posterad with Lig3: (0) absent; (1) present. For *Haematopinus* see Tröster (1990a, p. 20).

103 Lig5 of Tröster (1990a), from ventral side of head capsule to floor of preoral cavity: (0) absent; (1) present. For *Haematopinus* see Tröster (1990a, p. 20).

105 anterior tentorial arms: (0) absent; (1) present. “dorsal apodeme” of *Saldula* (Parsons 1963). The presence of vestigial anterior tentorial arms in *Saldula* was confirmed by Parsons (1964) based on the typical position (criterion of specific position) and the origin of the external antennal musculature (criterion of specific function). The “tentorium” of *Triatoma* (Barth 1952a,b, 1953a,b) is the hypopharynx. “dorsale Arme” of *Aphis* (Weber 1928); “Dorsalarme” of *Psylla* (Weber 1929a)

106 symmetry of anterior tentorial arms: (0) symmetrical; (1) asymmetric

107 fusion of anterior tentorial arms with corpotentorium: (0) absent; (1) present

108 posterior tentorial arms: (0) absent; (1) present. “ventrale Arme” of *Aphis* (Weber 1928); “Ventralarme” of *Psylla* (Weber 1929a)

109 length of posterior tentorial arm: (0) less than wide of corpotentorium; (1) longer than width of corpotentorium (minimal width between both arms if corpotentorium is absent)

111 dorsal tentorial arms: (0) absent; (1) present

112 corpotentorium/tentorial bar/tentorial bridge: (0) absent; (1) present

113 structure of corpotentorium: (0) membranous or as ligament; (1) sclerotized

115 paired hump-shaped corpotentorial protrusions: (0) absent; (1) present

118 clypeal ligament, “Clypealligament of Haub (1967) (connecting cephalic roof with anterior tentorial arm/Laciniadrüse): (0) absent; (1) present

119 antenna folded below head, received in groove (formed by gena): (0) absent; (1) present

120 origin of antennae: (0) between eyes and clypeus or at ocular level; (1) below eyes

121 antennal ledge (structure at right angle to antennnal base, Singh [1971, fig.1]): (0) absent; (1) present

122 antennal squama ("Antennenschuppe") (As) (Figs. 21B,C, 22D) (Risler 1951) below antennal base: (0) absent; (1) present

123 antennifer (mesal process formed by circumantennal ridge as abutment for antennal (scapal) base: (0) absent; (1) present. “dorsolateral corner of rim of antennal sclerite" of *Schizodactylus* (Khattar 1958).

125 swollen bulbous pedicellus (at least twice as wide as scapus): (0) absent; (1) present

126 number of antennomeres (all antennal segments): (0) 5 or more; (1) 4; (2) 3

127 antennal shape: (0) not aristate; (1) aristate

128 distal antennomeres (3rd + 4th) resembling a cupula enclosing its acorn: (0) absent; (1) present

129 antennal ring ("Antennenring") (Mickoleit 1963) (sclerotized ring between base of scapus and head capsule): (0) absent; (1) present. The ring-shaped antennal ring (“ringförmiger Antennalsklerit”) of *Oniscigaster* (Staniczek 2001) is apparently homologous with the antennal ridge. This also applies to the “antennal sclerite” of *Schizodactylus* (Khattar 1958). The “Antennenring” of *Thrips* is not explicitly described but compare fig. 1 of Risler (1957) with fig. 1 of Mickoleit (1963).

134 scapus sclerites: (0) absent; (1) present. “Skleritplättchen” of *Aeolothrips intermedius* (Moritz 1982b).

135 intercalary sclerite between scapus and pedicellus ("prepedicellite, pp") (Zrzavý 1990): (0) absent; (1) present

136 type of prepedicellite (Zrzavý 1990): (0) pp(I); (1) pp(II)

137 intercalary sclerites ("preflagelloid, pf" or "prebasiflagellite, pb") between antennomeres two and three (Zrzavý 1990): (0) absent; (1) present

138 type of preflagelloid/prebasiflagellite (Zrzavý 1990): (0) pf(I); (1) pf(II); (2) pf(IV); (3) pb. "cuticulärer Innenring" of *Aeolothrips intermedius* (Moritz 1982b). The sclerotized ring between pedicellus and flagellomere is a possible "synapomorphy of the condylognathous clade (Thysanoptera + Hemiptera)” according to Zrzavý (1990).

139 intercalary sclerites ("intraflagelloid, if") between antennomeres 3 and 4 (Zrzavý 1990): (0) absent; (1) present (if(I))

142 kidney-shaped sensory field on lateral side of pedicellus: (0) absent; (1) present

143 basal collar of antennomere three (and more distal segments in adults) (rupture-facilitating device; Seeger 1975): (0) absent; (1) present

144 functionality of rupture-facilitating device (Seeger 1975): (0) functional; (1) functionality absent or reduced

147 antennal tuft organs ("stalk with several finger-like projections in the tip", Cruz 1995) ("pit organ" of Cruz & Mateo 1996) inserted in disc-like depressions (Miller 1969): (0) absent; (1) present. Miller (1969), Slifer & Sekhon (1980), Clarke (1990), Piotrowski

(1992), Steinbrecht (1994), Cruz (1995), Cruz & Mateo (1996), and Arya & Singh (2012) suggested that the antennal tuft organ is a ground plan feature of Phthiraptera.

148 number of hairs of tuft organ (Miller 1969): (0) 4 to 7 (both head and body race of *Pediculus humanus*); (1) 8 to 10; (2) 12 to 15

149 antennal pore organs (two) (Miller 1969) or plate organs (Baker & Chandrapatya 1992): (0) absent; (1) present. Pore or plate organs are likely also part of the ground plan of Phthiraptera. These structures are also documented for single ischnoceran Philopteridae (Slifer 1976).

150 antennal sexual dimorphism, usually male antennomere three conical or with mesal hook (clamping device): (0) absent (see also Seeger 1975, zur Strassen & Göllner-Scheiding 2005); (1) present

153 0an3, M. tentorioscapalis lateralis: (0) absent; (1) present

154 0an4, M. tentorioscapalis medialis: (0) absent; (1) present

155 origin of extrinsic antennal muscles 0an1 and 0an2: (0) anterior tentorial arms; (1) head capsule; (2) dorsal tentorial arms; (3) corpotentorium; (4) anterior and dorsal tentorial arms; (5) anterior tentorial arms + head capsule; (6) dorsal tentorial arms + corpotentorium

158 0an8, M. intraflagellaris (primus): (0) absent; (1) present

159 0anx1, “M. intraflagellaris secundus”: (0) absent; (1) present.

160 mandibular articulation: (0) external; (1) internal (feeding stylets articulate within head capsule)

161 characteristic of external articulation: (0) base of mandible completely visible externally; (1) only part of mandibular base visible externally. Condition in *Trimenopon* unclear (mandibular base not visible in fig. 2 of Stöwe 1943).

162 condylus of mandibular base: (0) absent; (1) present

163 articulation with head capsule (external): (0) unicondylar (anterior articulation, Matsuda 1965); (1) dicondylic

166 spatial configuration of mandibles, maxillae and hypopharynx: (0) mandibles and maxillae laterad of hypopharynx, mandibular and maxillary articulations posterad hypopharyngeal tip; (1) mandibles and maxillae shifted craniad, articulations close to or anterad hypopharyngeal tip (von Kéler 1966a, p. 288)

167 functionality of mandibles: (0) both mandibles functional; (1) only left mandible functional (right one modified as "Tragarm des Pharynx", Mickoleit 1963)

168 mandibular shape: (0) resembling generalized mandible; (1) stylet-like; (2) conical and elongated; (3) divided into a globular to flattened ventral part and flattened to halfpipe dorsal region (Tröster 1990a) ("Mandibelplatte" and "Blutüberleitrinne", Ramcke 1965,

Hirsch 1986) (Figs. 25B–D); (4) thysanuroid type (elongate, oblique inner basal margin excavated, Matsuda 1965, p. 77)

170 symmetry of mandibles: (0) symmetric (e.g. Faucheux 1975); (1) asymmetric

171 function of mandibles: (0) biting; (1) piercing; (2) guiding device for piercing hypopharynx; (3) transport of liquids ("Blutüberleitrinne", e.g. Hirsch 1986) (von Kéler 1966a)

172 mandible with mesal indentation as recess for galea (e.g. Figs. 16D, 18B, 22D): (0) absent; (1) present (see Risler 1951 for summary of "Psocidae")

173 prostheca (brush-like process articulated with ventral surface of mandible): (0) absent; (1) present. The prostheca is absent in *Perla*. However, Chisholm (1962) documented a prostheca for other Plecoptera e.g. *Brachyptera risi* (MORTON, 1896) (Taeniopterygidae), and *Capnia bifrons* (NEWMAN, 1839) (Capniidae).

175 mandible/mandibular stylet enclosing lacinia (Figs. 12C–F, 14B,C): (0) absent; (1) present

176 laterocranial sclerotized connection of mandibular base and stipes: (0) absent; (1) present

177 vestige of the right mandibular base (Mickoleit 1963) (not identical with "Tragarm"): (0) absent; (1) present

178 protrusion of proximal mandibular part forming long and slender apodeme or tendon (a) (Fig. 4): (0) absent, (1) present

179 mesal parts of incisivi forming closed canal (von Kéler 1966a) ("Blutüberleitrinne", e.g. Hirsch 1986): (0) absent; (1) present

181 number of dendrites per mandibular dendritic canal (mdc) (Fig. 12B) or number of mandibular nerve branches (see also Cobben 1978): (0) 2; (1) 3; (2) 5; (3) 6

182 barb-like structures at mandibular apex: (0) absent; (1) present

183 incisivi (apical): (0) absent; (1) present

184 numbers of incisivi on left mandible: (0) 2; (1) 5; (2) 4; (3) 6; (4) 3. This character is unclear for *Haematomyzus* (Weber 1969) as the separation into incisivi and molar teeth is not possible.

185 numbers of incisivi on right mandible: (0) 2; (1) 5; (2) 4; (3) 6; (4) 3. This character is unclear for *Haematomyzus* (Weber 1969) as the separation into incisivi and molar teeth is not possible.

186 molar teeth: (0) absent; (1) present

187 shape of mandibular and maxillary feeding stylets in lateral view and resting position: (0) linear; (1) boomerang-shaped, arched antero-dorsally; (2) forming a loop posteriorly; (3) boomerang-shaped, arched dorso-caudally (see fig. 4 of Heming 1978)

188 structure of stylet loop: (0) major part or half of total length of stylets enclosed within labium in resting position, curved part dorsally directed; (1) major part of stylets lying within body, curved part caudally directed in resting position

189 mandibular lever (mdl) (Figs. 4D,E, 11A): (0) absent; (1) present. The lever arises as secondary formation of the stylet pouch (Parsons 1964). Thus, the homology to the prostheca as rudiment of the exopodite of the crustacean mandible is rejected (e.g. Bauernfeind 2005). “Protraktorarm" of *Aphis* (Weber 1928); “Artikulationshebel H1” of *Dactylosphaera* (Rilling 1960)

190 shape of mandibular lever: (0) equilateral triangle; (1) acute triangle, arm attached to mandible elongated; (2) acute triangle, arm attached to mandible elongated and caudally directed (Rieger 1976); (3) quadrangular; (4) bar-shaped, (5) curved triangle; (6) V- to Y-shaped (base opposite to stylet)

193 mandibular gnathal pouch: (0) absent; (1) present

194 exposure and formation of mandibular gnathal pouch: (0) internalized, maxillae and mandibles hidden in separate gnathal pouches; (1) left mandible enclosed in pouch formed by anteclypeal wall, labrum, stipes and hypopharynx

195 0md1, M. craniomandibularis internus: (0) absent, (1) present

196 0md2, M. craniomandibularis externus anterior: (0) absent, (1) present

197 0md3, M. craniomandibularis externus posterior: (0) absent, (1) present

198 0md4, M. hypopharyngomandibularis: (0) absent, (1) present

199 insertion of 0md4: (0) inside mandibular lumen; (1) restricted to the posterior outer edge

200 0md5, M. tentoriomandibularis lateralis superior: (0) absent, (1) present

201 0md6, M. tentoriomandibularis lateralis inferior: (0) absent, (1) present

203 0md8, tentoriomandibularis medialis inferior: (0) absent, (1) present.

204 0mdx1, mandibular retractor in Hemiptera: (0) absent, (1) present.

205 insertion of 0mdx1: (0) mandibular base or posterior tendon; (1) mandibular lever

206 0mdx2, mandibular retractor in Hemiptera: (0) absent, (1) present

207 0mdx3, protractor of mandibular lever in Hemiptera: (0) absent, (1) present

208 0mdx4, protractor of mandibular lever in Hemiptera: (0) absent, (1) present

209 0mdx5, protractor of mandible in Hemiptera: (0) absent, (1) present

210 insertion of 0mdx5: (0) mandibular stylet; (1) mandibular lever

213 laciniae: (0) absent; (1) present. The cylindrical lacinia of *Trimenopon* described by Stöwe (1943) is partly located in a mandibular depression and moved by a single muscle M2. Such a configuration is otherwise unknown in Amblycera and Psocoptera. Therefore, it is likely that the “lacinia” described by Stöwe (1943) is in fact the galea. This is supported by a comparison with *Gliricola* (Risler & Geisinger 1965) or *Liposcelis*

(Fig. 18B), where a voluminous galea is partly enclosed by the mesal edge of the mandible and moved by a single stipito-galeal muscle. Nevertheless, the condition of the lacinia of *Trimenopon* is not fully clarified, and this also applies to *Haematomyzus.* Weber (1969) mentioned maxillary vestiges ("Maxillenreste") without referring to specific parts and maxillary muscles are completely absent. This greatly impedes the homologization (in contrast to Grimaldi & Engel 2005).

214 articulation of lacinia: (0) external; (1) internal

215 structure of lacinia: (0) cylindrical or flattened, not stylet-like; (1) stylet-like

216 shape of stylet-like lacinia (la): (0) needle-like (Fig. 5C–E); (1) chisel-shaped and robust (Fig. 5A); (2) shifted into interior of head as valve for lacinia gland ("Lacinia-Drüse")/maxillary gland (Tröster 1990a)

217 apex of lacinia: (0) with single tip or blunt apex; (1) bifurcated; (2) trifurcated

218 setae on tip of lacinia: (0) absent; (1) present

219 barb-like structures/dentations on tip of lacinia: (0) absent; (1) present

220 connection of lacinia and stipes: (0) lacinia articulated with stipes; (1) lacinia detached from stipes

221 interlocking grooves of laciniae forming one or two canal(s) (e.g. Figs. 11D, 12E, 14C): (0) absent; (1) present

222 salivary canal (sa) (Figs. 12D–F, 14C): (0) formed by interlocked maxillary stylets/laciniae; (1) formed by labial groove (glossa/prementum) proximally and by interlocked laciniae distally (fused with food canal)

223 fusion of salivary canal with food canal: (0) absent (separate salivary canal); (1) present. For Thysanoptera see also *Haplothrips* (Heming 1978) and *Frankliniella* (Hunter & Ullman 1992).

224 formation of salivary canal (Figs. 12D–F, 14C): (0) indentation of right maxilla; (1) indentation of left maxilla; (2) mutual or variable along entire maxillary length

225 food canal (fc) formed by laciniae (Figs. 12D–F, 14C): (0) absent; (1) present

226 shape of interlocked maxillary stylets in cross-section (Figs. 12D–F, 11D, 14C): (0) compressed dorso-ventrally; (1) compressed laterally; (2) circular

230 cardo (cd) (e.g. Fig. 5C): (0) absent; (1) present

231 cardo divided into mesal proxicardo and lateral disticardo (Beutel & Weide 2005): (0) absent; (1) present. "inner juxtacardo and the outer veracardo" of *Schizodactylus* (Khattar 1958).

232 fusion of cardo with stipes: (0) absent; (1) present

233 separated minute sclerite of cardo (cds) (Fig. 5C): (0) absent; (1) present.

234 stipes (st) as well defined element (maxillary plate of Hemiptera) (e.g. Figs. 5, 14A, 15B, 17C): (0) absent; (1) present

235 fusion of stipes or cardo-stipes with ventral head capsule and labium (Tröster 1990a) (Fig. 19C): (0) absent; (1) present

236 distal stipital region enclosed by distal mesal wall of labrum (see also Mickoleit 1963, p. 114): (0) absent; (1) present

242 galea (ga) (e.g. Fig. 5): (0) absent, (1) present. Masumoto & Nagashima (1993) rejected the homology of the "distal lobe of the maxilla" of *Psococerastis* with the galea. However, Yoshizawa (2005, p. 6) showed that the lobe is indeed homologous to the galea. For an interpretation of the “lacinia” of *Trimenopon* see character 113.

244 galea apically divided into two lobes or spines: (0) absent; (1) present. “adoraler + aboraler Incisivus der Galea” of *Oniscigaster* (Staniczek 2001)

245 galea divided into basigalea and distigalea (Beutel et al. 2010): (0) absent; (1) present

247 galea: (0) mesal side glabrous; (1) mesal side equipped with teeth or posteriorly directed barbed hooks (Fig. 5B)

249 ventral part of galeae as guiding device (von Kéler 1966a) for piercers (galeal guiding folds ["Führungsfalten"] and dorsal feeding bristle of hypopharynx, Tröster 1990a): (0) absent; (1) present

251 fusion of galea with ventral side of mandible (Figs. 25C,D): (0) absent; (1) present

252 fusion of caudal region of galea fused with tip of dorsal hypopharynx (Tröster 1990a): (0) absent; (1) present

253 palpifer: (0) absent; (1) present

254 palpus maxillaris (maxillary palp): (0) absent; (1) present

255 segmentation of maxillary palp: (0) 2-segmented; (1) 3-segmented; (2) 4-segmented (e.g. 17C, 19C); (3) 5-segmented. According to Matsuda (1965) the maximum number of segments in Thysanoptera is eight.

256 maxilllary lever (mxl) (e.g. Figs. 5C–E, 11B): (0) absent; (1) present (bar-shaped to curved). According to Verma et al. (1973) the maxillary lever of Nepomorpha “is very much reduced”. The maxillary lever of *Belostoma* mentioned in Swart & Felgenhauer (2003) is in fact the mandibular lever. “maxillarer Artikulationshebel H2” of *Dactylosphaera* (Rilling 1960); “Artikulationshebel” of *Thrips* (Risler 1957). The "cranial apodeme of lacinia" of *Psocus* (Cope 1940) is apparently a lacinial retractor.

257 connection of maxillary lever: (0) with hypopharyngeal wing or hypopharynx; (1) with stipes/head capsule (spacer)

258 maxillay lever as muscle attachment side: (0) absent; (1) present

259 maxillary lever as muscle attachment side for: (0) retracor; (1) protractor; (2) both protractor and retractor

261 0mx1, M. craniocardinalis: (0) absent; (1) present

263 origin of 0mx2, M. craniolacinialis: (0) vertex; (1) posterior tentorial arm; (2) postocciput; (3) gena; (4) both postocciput and postgena
264 0mx3, M. tentoriocardinalis: (0) absent; (1) present
265 0mx4, M. tentoriostipitalis anterior: (0) absent; (1) present
266 0mx5, M. tentoriostipitalis posterior: (0) absent, (1) present
267 origin of 0mx5, M. tentoriostipitalis posterior: (0) tentorium; (1) head capsule
268 0mx6, M. stipitolacinialis: (0) absent; (1) present
269 0mx7, M. stipitogalealis: (0) absent; (1) present
270 0mx8, M. stipitopalpalis externus: (0) absent; (1) present
271 origin of 0mx8, M. stipitopalpalis externus: (0) stipital region; (1) medial wall of stipes and rudiment of right mandible (=Tragarm des Pharynx); (2) head capsule (in general its ventral region)
272 0mx9, M. stipitopalpalis medialis: (0) absent; (1) present
273 0mx10, M. stipitopalpalis internus: (0) absent; (1) present
274 0mx12, M. palpopalpalis maxillae primus: (0) absent; (1) present
275 0mx13, M. palpopalpalis maxillae secundus: (0) absent; (1) present
276 0mx14, M. palpopalpalis maxillae tertius: (0) absent; (1) present
277 0mx15, M. palpopalpalis maxillae quartus: (0) absent; (1) present
278 0mxx1, “M. craniolacinialis secundus”: (0) absent; (1) present
279 0mxx2, “M. palpopalpalis maxillae secundus secundus”: (0) absent; (1) present
280 0mxx3, retractor of maxillary lever: (0) absent; (1) present
281 origin of 0mxx3: (0) tentorium; (1) cranium
282 0mxx4, “M. lacinio-mandibularis”: (0) absent; (1) present
283 0mxx5, protractor of maxillary lever: (0) absent; (1) present
284 0mxx6, “M. tentorio-lacinialis”: (0) absent; (1) present
285 0mxx7, muscle operating maxillary gland: (0) absent; (1) present
286 0mxx8, “M. palpopalpalis maxillae primus secundus”: (0) absent; (1) present
287 0mxx9, “M. stipitogalealis secundus”: (0) absent; (1) present
288 attachment of base of labium: (0) anterior part of head capsule or anterior to gula; (1) cervical region (neck)
289 fusion of labium with pleuro- and hypostomal margin of head capsule forming a "poche gnathale" (von Kéler 1966a) and with labrum and clypeus (Mey 2005): (0) absent; (1) present
290 procoxae covering basal part of labium, labium moved indirectly by prosternal movement or "partial accretion of bottom labium with ventral prothorax" (Drohojowska 2009): (0) absent; (1) present
291 labium forms tube-like sheath for mandibles and laciniae: (0) absent; (1) present

292 number of segments of labial rostrum: (0) 1; (1) 3; (2) 4; (3) 2. The number of segments in the heteropteran family Schizopteridae varies between three and four. The paired sclerites of *Scolops* (Kramer 1950) between segment I and III are interpreted as the second labial segment. However, ontogenetic studies are necessary to confirm that these structures are not homolgous to intercalary sclerites.

293 labial intercalary sclerites between third and fourth segment of labial rostrum (single pair): (0) absent; (1) present

295 clasping organs at tip of labium (clasper): (0) absent; (1) present. The documentation of the “holdfast mechanism” of *Lethocerus* (Parsons 1968) is fragmentary and the homology with clasping devices uncertain.

297 interlocking of edges of labial groove (Fig. 14C): (0) absent; (1) present. “fingerförmige Fortsätze” of *Psylla* (Weber 1929a)

298 tripartite apex of labial rostrum or apical closing lid of terminal labial segment (see also "apical plate" of Cobben [1978] for *Ochterus*, *Gelastocoris*, *Nepa*, *Gerris*, *Hydrometra*, and Wenk et al. [2010] for *Triatoma*): (0) absent; (1) present. "sklerotisierte Gleitplatte für die Stechborsten der Labialrinne" of *Corixa* (Benwitz 1956); “terminal plate on stylet groove" of *Lethocerus* (Parsons 1968).

299 bar-shaped and unpaired apodeme of second labial segment (also applicable when segment I is reduced): (0) absent; (1) present. “Ap2a” of *Ochterus* (Rieger 1976); "mediane Sehne" of *Corixa* (Benwitz 1956); “oblique plate” of *Gelastocoris*, *Lethocerus*, *Saldula* (Parsons 1959, 1962, 1968); "crumena" of *Trialeurodes* (Weber 1935); “Lbap” of *Aleurolobus*, *Platypleura*, *Oxyrhachis*, and *Melicharia* (Singh 1971).

300 suspensory plate (single broad lamella at base of first labial segment, partly fused with hypopharyngeal wings, salivary pump, and first labial segment) (Parsons 1959). The suspensory plate is of hypopharyngeal origin and likely developed as extension of the hypopharyngeal sublingual sclerites (Parsons 1964), or alternatively “from the labial wall of the salivarium of the orthopteroid head.” (Puchkova 1970): (0) absent; (1) present. “Aufhängeblatt” of *Ochterus* (Rieger 1976); “transparent sclerotized area” of *Gerris* (Cranston & Sprague 1961).

301 glossa (gl) (e.g. Figs. 6A,B, 15C, 17C): (0) absent; (1) present: The glossa of *Haematopinus* shown by Ramcke (1965) is in fact part of the membranous anterodorsal part of the "Stacheldrüse" according to Tröster (1990a) (see below).

302 number of glossae: (0) 2; (1) 1

303 Y-shaped sclerite connected with prementum for support of glossa (GSkl) (Fig. 6B): (0) absent; (1) present. "Gabelsklerit" of *Thrips* (Risler 1957), “sclerites of prementum” of *Psocus* (Cope 1940).

304 two sclerotized internal rods of glossa: (0) absent; (1) present: “Carina” of glossae of *Myrsidea* (Buckup 1959).

305 paraglossae (pgl) (e.g. Figs. 6A,B, 15C, 17C): (0) absent; (1) present. “ventral lobe or ligula of labium” of *Troctes* (Noland 1924). Ramcke (1965) argued that the bifurcated tips of the ventral premental stylet of *Haematopinus* are the apices of the paraglossa and labial palp, respectively. This was not confirmed in other studies (e.g. Tröster 1990a).

307 conical lobe between paraglossae, formed by extension of median part of glossae, covering glossal groove (see Yoshizawa 2005): (0) absent; (1) present

308 paraglossae enclosing apex of labrum/apex of mouth cone in resting position (see figs. 3a–4a in Hunter & Ullman 1989; and fig. 7 in Heming 1978): (0) absent; (1) present

309 subdivision of postmentum into submentum and mentum: (0) absent; (1) present. The “mentum” of *Troctes* (Noland 1924) bears the labial palps and is consequently the prementum. The submentum of *Troctes* (Noland 1924) is the postmentum.

310 sclerotization of submentum: (0) absent, submentum membranous; (1) present

312 prementum folded, forming salivary canal, continued by glossa: (0) absent; (1) present (Matsuda 1965; Yoshizawa 2005). "internal keel-like structure" of *Perla* (Chisholm 1962).

313 ventral piercing bristle (ls) (Figs. 6D, 26B,C) (formed by prementum) (Matsuda 1965, Haub 1983, Tröster 1990a): (0) absent; (1) present

314 limes labialis (Stojanovich 1945), transverse sclerotized bar or fold in middle region of internal floor of trophic sac as muscular origin, situated at "the posterior border of the prementum just anterior to the fold between mentum and submentum" (Stojanovich 1945) (Figs. 6D, 26C): (0) absent; (1) present. “Lasche” of *Haematopinus* (Ramcke 1965)

316 posterior end of prementum transformed into "Ventralkolbenbogen" with paired "Ventralkolben" (von Kéler 1966a), dorsal and ventral apodeme of ventral piercing bristle (Figs. 6D, 25I): (0) absent; (1) present. "ventrales Apodem des ventralen Stiletts" and "dorsales Apodem des ventralen Stiletts" of *Haematopinus* (Ramcke 1965) and *Phthirus* (Hirsch 1986).

317 labial palp: (0) absent; (1) present

318 segmentation of labial palp: (0) 5-segmented; (1) 2-segmented; (2) single segment (Figs. 17C, 19C, 21C); (3) 3-segmented

324 true crumena (membranous pouch hosting feeding stylets within insect body and outside of labial groove; different from maxillary sac) (cru) (Figs. 10G,H, 11D): (0) absent; (1) present

325 ring muscle layer of crumena (see also Weber 1929b for *Perissopneumon*): (0) absent; (1) present

326 movement of labium or mouth cone during initialization of feeding (Weber 1929): (0) no deformation; (1) contraction; (2) distally bent between labial segments II and III, proximally bent between segments I and II (see fig. 96 in Jordan 1972); (3) retraction of labium into head capsule/prothorax with simultaneous telescoping movements; (4) bent between basal and second segment and/or additional retraction; (5) partly unfolding

330 0la4, M. postoccipitopraementalis primus: (0) absent; (1) present

331 0la4, M. postoccipitopraementalis secundus: (0) absent; (1) present

332 0la5, M. tentoriopraementalis: (0) absent; (1) present

333 0la8, M. submentopraementalis: (0) absent; (1) present

334 origin of 0la8, M. submentopraementalis: (0) postementum; (1) gula; (2) obturaculum. Not applicable for *Zorotypus* (Beutel & Weide 2005) as one partition originates from the gula and the other from the postmentum.

335 insertion of 0la8, M. submentopraementalis: (0) medial base of prementum; (1) laterally on ventral apodeme of ventral piercer; (2) "Laschenapodem" (Ramcke 1965)

336 0la11, M. praementoparaglossalis: (0) absent; (1) present

337 0la12, M. praementoglossalis: (0) absent; (1) present

338 0la13, M. praementopalpalis internus: (0) absent; (1) present

339 0la14, M. praementopalpalis externus: (0) absent; (1) present

340 0la16, M. palpopalpalis labii primus: (0) absent; (1) present

341 0la17, M. palpopalpalis labii secundus: (0) absent; (1) present

342 0lax1, labial abductor of Hemiptera: (0) absent; (1) present

343 0lax2, labial adductor of Hemiptera: (0) absent; (1) present

344 origin of 0lax2: (0) hypopharynx; (1) border region of 1st and 2nd labial segment or shifted to 1st segment including suspensory plate

345 0lax3, labial adductor of Hemiptera: (0) absent; (1) present

346 0lax4, labial adductor of Hemiptera: (0) absent; (1) present

347 0lax5, labial adductor of Hemiptera: (0) absent; (1) present

348 0lax6, labial adductor of Hemiptera: (0) absent; (1) present

350 0lax8, labial transversal muscle of Hemiptera: (0) absent; (1) present

351 0lax9, labial transversal muscle of Hemiptera: (0) absent; (1) present

352 0lax10, labial transversal muscle of Hemiptera: (0) absent; (1) present

353 0lax11, basal labial muscle of Hemiptera: (0) absent; (1) present

354 0lax12, muscle of labial crumena of Hemiptera: (0) absent; (1) present

355 0lax13, basal labial muscle of Hemiptera: (0) absent; (1) present

356 0lax14, labial abductor of Hemiptera: (0) absent; (1) present

357 origin of 0lax14: (0) hypopharynx; (1) cranium; (2) tentorium

359 0lax16, transversal labial muscle of Hemiptera: (0) absent; (1) present

360 0lax17, basal labial muscle of Hemiptera: (0) absent; (1) present

361 0lax18, additional set of transversal musles at distal end of third labial segment of Hemiptera: (0) absent; (1) present

362 0lax19, basal labial muscle of Hemiptera: (0) absent; (1) present

364 0lax21, “M. palpopalpalis labii primus lateralis”: (0) absent; (1) present

366 0lax23, labial muscle of Hemiptera: (0) absent; (1) present

367 movability of labrum: (0) absent; (1) present

368 shape of labrum: (0) transverse or ± rectangular, with slightly convex or straight anterior margin, with or without indentation; (1) narrowed, triangular, tongue-shaped; (2) haustellum (hau) (Figs. 23, 24, 27C) (lateral margins convoluted ventrolaterally, von Kéler 1966a); (3) ± rectangular with deep median incision

369 labrum equipped with teeth: (0) absent; (1) present (Haustellarzähne of Anoplura, von Kéler 1966a) (hauto) (Figs. 24, 27C)

370 "Labralleiste" situated at labral base (Mickoleit 1963): (0) absent; (1) present. “Labralsklerit” of *Oniscigaster* (Staniczek 2001); “pre-labrum” of *Perla* (Chisholm 1962); “sklerotisierte Cuticularpartie” of *Myrsidea* (Buckup 1959); "Skleritspange" of *Pseudomenopon* (Haub 1967); “Labralsklerite” of *Trochiloecetes* (Haub 1983); “Querspange” of *Bovicola* (Risler 1951); “ventral carina” of *Columbicola* (Smith 2001); “Skleritspange” of *Hybophthirus* (Tröster 1990a); “Skleritwulst” of *Phthirus* (Hirsch 1986)

371 labrum forming sheath for mandibles and maxillae: (0) absent; (1) present

372 separation of labral tip from rest of labrum by membrane or ledge: (0) absent; (1) present

373 0lb1, M. frontolabralis: (0) absent; (1) present

374 origin of 0lb1, M. frontolabralis: (0) clypeofrons; (1) origin shifted to right side, one portion on clypeofrons, other on right rudiment of anterior tentorial arm

375 0lb2, M. frontoepipharyngalis: (0) absent; (1) present

376 topography of 0lb2, M. frontoepipharyngalis: (0) symmetrical; (1) only present on left side

377 function of 0lb2, M. frontoepipharyngalis: (0) movement of labrum; (1) involved in locking/protrusion of the mandible

378 0lb5, M. labroepipharyngealis: (0) absent; (1) present

379 topography of 0lb5, M. labroepipharyngealis: (0) origin shifted to right part of labrum, insertion on epipharynx; (1) origin on lateral wall of clypeofrons and vestige of right mandible (="Tragarm des Pharynx"), insertion distally on labral tip; (2) symmetrical; (3)

unpaired muscle along medio-longitudinal body axis or several bundles arranged as a median row

380 0lbx1, “M. longitudinalis epipharyngealis dorsalis”: (0) absent; (1) present

381 0lbx2, “M. tentorio-epipharyngealis”: (0) absent; (1) present

382 structure of hyopharynx: (0) unmodified ("tongue-shaped") and movable; (1) not tongue-shaped (hypopharyngeal wings present) (suspensorial sclerites; "Randleisten der Speichelrinne" [Risler 1957]; "Führungsleiste der Laciniae" [Mickoleit 1963]; see also p. 9 of Heming [1978]; “Tentorium” of *Triatoma* [Barth 1952a,b]).

383 additional wings of hypopharynx ("Flügelapodem" of Risler 1957 and Mickoleit 1963; "hypopharyngeal fulturae" of Heming 1978) (Fig. 7D): (0) absent; (1) present

384 Cibarialsklerit/sitophore (sit) (e.g. Figs. 7A–C, 18G, 20E) (continuous sclerotized middle part of hypopharynx, Buckup 1959): (0) absent; (1) present

385 sitophore with fenestration(s) (opening for cibarial sense organ) covered by membranes (Fig. 7C): (0) absent; (1) present (character of Haub 1972)

387 sitophore of hypopharynx as salivary pumping chamber (Snodgrass [1938] homologized the sitophore with the ventral wall of the salivary pump) (e.g. Figs. 7D,E): (0) absent; (1) present

388 orientation of hypopharynx (including pumping chamber): (0) dorso-ventral; (1) craniocaudal

389 formation of salivary pumping chamber or salivarium: (0) hypopharyngeal; (1) between hypopharynx and labium

390 sclerotized hypopharyngeal ring on roof of salivarium (salivary pump), origin of membranous piston (Mickoleit 1963; Matsuda 1965): (0) absent; (1) present

391 opening of salivarium/pumping chamber: (0) between maxillary stylets; (1) glossal region or tip of prementum

392 piston (pis) (Figs. 7D,E, 12B): (0) absent; (1) present

393 salivary ducts associated with hypopharynx (sd) (Fig. 12B): (0) absent; (1) present

394 oral arms of hypopharnyx (Yoshizawa 2005) (or) (e.g. Figs. 7A,B, 16D, 20E): (0) absent; (1) present. "suspensorial tendon" as attachment side of M. frontohypopharyngalis of *Osmylus* (Beutel et al. 2010); “apex of the suspensorium at the anatomical mouth” of *Zorotypus* (Beutel & Weide 2005); “posterior arm of suspensorial sclerite” of *Perla* (Chisholm 1962); “supports which help to attach the sclerite in the mouth” of *Troctes* (Noland 1924); “Hinterarme des Cibarialsklerits” of *Trochiloecetes* (Haub 1983); “posterior cornu” of *Trimenopon* (Stöwe 1943)

396 length of oral arm ("Hinterarme" of Haub 1972): (0) shorter than length of sitophore (or body of hypopharynx); (1) longer than length of sitophore (see also Haub 1972)

397 median cone (bar) located between bases of oral hypopharyngeal arms ("Steg" of fig. 2 of Haub 1972) (Figs. 7B,C): (0) absent; (1) present

398 Matsuda's posterior arms of hypopharynx (1965p, p. 135 fig. 53B) = Haub's (1967, 1983) "Vorderarme des Cibarialsklerits" or "Dorsaler Hypopharynx" (po) (e.g. Figs. 7A–C): (0) absent, (1) present. "hypopharyngeal rod" of *Macroxyela* (Beutel & Vilhelmsen 2007); “basal lateral sclerite” of *Schizodactylus* (Khattar 1958); “anterior arm of suspensorial sclerite” of *Perla* (Chisholm 1962); “posterior horn of oesophageal sclerite” of *Troctes* (Noland 1924); “Vorderarme des Cibarialsklerits” of *Gliricola* (Risler & Geising 1965), *Myrsidea* (Buckup 1959), and *Pseudomenopon* (Haub 1967); “anterior cornu” of *Trimenopon* (Stöwe 1943); “dorsale laterale Längsleisten der Stechborstenscheide” of *Hybophthirus* (Tröster 1990a)

399 length of posterior hypopharyngeal arms ("Vorderarme" of Haub 1972) (see also Haub 1972): (0) shorter than length of sitophore or body of hypopharynx; (1) longer than length of sitophore

400 fusion of posterior hypopharyngeal arms: (0) absent; (1) present. The condition is unclear in *Ornithobius*. Haub (1971) mentioned the anterior arms ("Vorderarme") of the hypopharynx but did not label them in his figure 18. They are apparently fused with each other (see also fig. 15 of Haub 1967).

402 posterior hypopharyngeal arms forming guiding device for ventral part of hypopharynx (Fig. 7F): (0) absent; (1) present

403 loral arm of hypopharynx (Matsuda 1965, Yoshizawa 2005): (0) absent; (1) present. “mandibular arm of suspensorium” of *Schizodactylus* (Khattar 1964); “basal rod” of hypopharynx of *Perla* (Chisholm 1962)

404 swollen paired ovoid sclerites (Matsuda 1965, p. 134) (“lingual sclerites” of Snodgrass 1944; “Fulturae” of von Kéler 1966a, part of the ventral hypopharynx of Haub 1983) (see also Yoshizawa 2005) (ov) (e.g. Figs. 7A, 16F, 22F): (0) absent; (1) present. The ovoid sclerites are homologous with the "labial glands" of *Troctes*, as they are similar in shape and position (criterion of position) and also connected by ligaments to the hypopharynx (criterion of specific quality and structure) (Noland 1924).

405 ovoid sclerites forming guiding device for hypopharyngeal and labial feeding stylets (Tröster 1990a) (Fig. 7F): (0) absent; (1) present

407 paired filamentous ligaments (liov) (e.g. Figs. 7A, 16F, 22E) ("Chitinfaden" of Haub 1972) connecting sitophore and ovoid sclerite (fig. 53 of Matsuda 1965), part of ventral hypopharynx (Haub 1983): (0) absent; (1) present

408 region of fusion of paired filamentous ligaments (see also Haub 1972) (Figs. 7A,B): (0) at level of sitophore; (1) at level of ovoid sclerites

409 suspensorium: (0) chitinous clasps or rods attached to hypopharyngeal body or not recognizable as individual structures; (1) elongated and wing-like

410 ventral part of hypopharynx transformed into dorsal piercing bristle or hypopharyngeal stylet (hs) (Figs. 7F, 26B,C) ("maxillary stylet" of Young 1953) (Matsuda 1965; Haub 1983; Tröster 1990a): (0) absent; (1) present. "dorsale Stechborste" of *Hybophthirus* (Tröster 1990a)

411 dorsal guiding rim of stylets ("dorsale Führungsrinne der Stechborsten") (sclerotized stripe in the roof of the ventral hypopharynx, reaching to the tip of the piercer (“Stachel”)) (dF) (Fig. 25F): (0) absent; (1) present

413 median salivary stylet (Matsuda 1965) (shs) (Figs. 7F, 26B,C), origin either hypopharyngeal (Schölzel 1937; Ramcke 1965) or labial (Stojanovich 1945; Young 1953) (hypopharyngeal bristle, labial bristle and salivary stylet together forming the piercer ("Stachel"), von Kéler 1966a): (0) absent; (1) present. "Speichelrohr" of *Haematopinus* (Ramcke 1965); "Speichelrinne des Hypopharynx" of *Hybophthirus* (Tröster 1990a)

415 piercer sheath (dps + vps) formed by dorsal part of hypopharynx dorsally and ventral prementum on ventral side, the latter partly folded into head capsule, membrane separating pre- and postementum elongated to ventromedian membranous bulge of anterior head capsule ("ventromedianen Membranwulst der vorderen Kopfkapsel") (mebu) (Tröster 1990a) (e.g. Figs. 6D, 24C, 26B): (0) absent; (1) present. "Stachelscheide" of *Haematopinus* (Ramcke 1965)

416 lateral ridge of stylet sheath ("Lateralleiste der Stechborstenscheide") with origin on lateral limes labialis (Tröster 1990a): (0) absent; (1) present

417 fusion of hypopharyngeal wings or hypopharynx with tentorium (i.a. posterior arms) dorsally: (0) absent; (1) present

419 hypopharynx with grooves as guiding devices for mandibles/maxillae (i.a. feeding stylets): (0) absent; (1) present

420 water vapor uptaking device (ovoid sclerites + filament perforating cibarial sclerite and forming connection between cibarium and salivarium) (see also Rudolph 1982, 1983 and Yoshizawa 2005): (0) absent; (1) present

421 sitophore (sit, cibarial sclerite, esophageal sclerite) acting as mortar, counterpart of epipharyngeal sclerite ("mortar and pestle apparatus" of Matsuda [1965]) (e.g. Figs. 18B,G, 22E,F): (0) absent (sitophore shovel-like); (1) present (sitophore as mortar) (Snodgrass [1938] argued that the sitophore in Hemiptera is the pumping chamber). The mortar and pestle apparatus is absent in the Amblycera examined, but Symmons (1952) documented a mortar-like sitophore of *Gyropus ovalis* BURMEISTER, 1838 (Gyropidae, Amblycera).

422 distal region of hypopharynx with thorns or bristles: (0) absent; (1) present. Risler & Geising (1965) addressed the two clubbed lingual sclerites as this region in *Gliricola* ("Lingualsklerite"), whereas Haub (1967) considered it as the apical hypopharyngeal region near to the superlingua in his study on *Pseudomenopon*. In comparison to *Trimenopon* (Stöwe 1943) it appears likely that the lingual sclerites of *Gliricola* include the superlinguae.

423 lingua (li) (Figs. 7A,B): (0) absent; (1) present

424 superlingua (sli) (Figs. 7A,B): (0) absent; (1) present

427 0hy1, M. frontooralis: (0) absent; (1) present

428 0hy1, M. frontooralis including "Ligament of Denis" (from laterodorsal side of clypeus to oral arms of hypopharynx): (0) absent; (1) present

429 0hy2, M. tentorioralis: (0) absent; (1) present

430 origin of 0hy2, M. tentorioralis: (0) tentorium; (1) head capsule, i.a. epistomal sulcus

431 0hy3, M. craniohypopharyngealis: (0) absent; (1) present

432 0hy4, M. postoccipitalohypopharyngealis: (0) absent; (1) present

433 origin of 0hy4, M. postoccipitalohypopharyngealis: (0) postoccipital region; (1) gena

434 0hy4, M. postoccipitalohypopharyngealis folded in resting position: (0) absent; (1) present

435 0hy5, M. tentoriosuspensorialis: (0) absent; (1) present

436 0hy7, M. praementosalivaris anterior: (0) absent; (1) present

437 0hy8, M. praementosalivaris posterior: (0) absent; (1) present

438 0hy9, M. oralis transversalis: (0) absent; (1) present

440 0hy12, M. hypopharyngosalivaris: (0) absent; (1) present

441 origin of 0hy12, M. hypopharyngosalivaris: (0) head capsule; (1) hypopharynx; (2) corpotentorium

442 0hyx1, “M. protractor hypopharyngis”: (0) absent; (1) present

443 0hyx2, “tentorial ligament”: (0) absent; (1) present

444 0hyx2, “tentorial ligament”: (0) unpaired; (1) paired

446 0hyx4, “M. hypopharyngo salivaris secundus”: (0) absent; (1) present

447 0hyx5, “M. hypopharyngo salivaris tertius”: (0) absent; (1) present

449 0hyx7, “M. hypopharyngo salivaris quintus”: (0) absent; (1) present

453 tormae: (0) absent; (1) present

454 epipharyngeal sclerite: (0) absent; (1) present. “Dorsalplatte” of *Haematomyzus* (Weber 1969)

455 number of epipharyngeal sclerites: (0) 1; (1) 2. “EpSkl” and “EpNSkl” of *Bovicola* (Risler 1951)

456 epipharyngeal sclerite developed as pistill of "mortar and pestle" apparatus (summarized in Matsuda 1965) (epp) (Figs. 18B, 22E): (0) absent; (1) present

457 distal part of epipharynx or anterior epipharyngeal sclerite developed as sclerotized halfpipe (Haub 1983): (0) absent; (1) present

458 fulcrum in roof of haustellum (triangular posterior epipharyngeal elongation with paired apodemes [von Kéler 1966a], not homologous to the two epipharyngeal sclerites) (pal) (Figs. 25B–E): (0) absent; (1) present. “palatum” of *Haematopinus* (Ramcke 1965) and *Phthirus* (Hirsch 1986)

459 Lig1 connecting posterior side of fulcrum with dorsal head capsule near frontal sutures (Tröster 1990a): (0) absent; (1) present

468 inter-pharyngeal locking mechanism (Ullman & McLean 1986; Hunter & Ullman 1994): (0) absent; (1) present

469 "inter-pharyngeal" locking mechanism (see also Ullman & McLean 1986; Hunter & Ullman 1994), (other than mortar and pestle apparatus): (0) epipharynx with protuberances interlocking with hypopharynx; (1) hypopharynx with protuberances interlocking with epipharynx; (2) epipharynx with ridges interlocking with hypopharynx

470 latero-ventral protrusion of epipharynx fitting into grooves of lacina (see also figs. 3–4 of Hunter & Ullman 1994): (0) absent; (1) present.

471 epipharyngeal triturating devices: (0) absent; (1) present. Epipharyngeal plates (“Epipharyngeale Platten“) of *Ochterus* (Rieger 1976)

472 epipharyngeal brush (arrow in Fig. 16C) ("a brush of microtrichia which interacts with the mandibles", Beutel & Vilhelmsen [2007]) correlated with microphagous feeding habit: (0) absent; (1) present

473 orientation of floor of food pump: (0) ventral; (1) dorsal; (2) vertical

474 precibarium, prepharynx (narrow canal situated between food canal of maxillae and cibarium): (0) absent; (1) present

476 "Mundvorraum" (formed by cranial elongation of gena, postgena, and pleurostomal region [von Kéler 1966a]): (0) absent; (1) present. “Prästoma” of *Haematomyzus* (Weber 1969)

478 palatum cibariale (von Kéler 1966a), paired folds enclosing epipharyngeal sclerite, fusing to single fold, almost reaching cibarial floor: (0) absent; (1) present. “epipharyngopharyngeal lobe” of *Macroxyela* (Beutel & Vilhelmsen 2007); "Cibarialgaumensklerit" of *Hybophthirus* (Tröster 1990a)

480 devorium (part of anterior pharynx bent anterad [von Kéler 1966a]): (0) absent; (1) present. "Schlucktasche" of *Hybophthirus* (1990a)

482 separation of pharynx and cibarium by sclerotized clasp: (0) absent; (1) present

483 distinct bent of pharynx (switch from dorso-ventral orientation to a cranio-caudal): (0) absent; (1) present

484 ring muscle layer of food pump/prepharynx: (0) absent; (1) present. 34 of *Pseudomenopon* (Haub 1967); M. circulares 1+2+3 of *Trochiloecetes* (Haub 1983); 33a+33b of *Bovicola* (Risler 1951); 17 of *Haematomyzus* (Weber 1969)

485 0ci1, M. clypeopalatalis: (0) absent; (1) present

486 0bu1, M. clypeobuccalis: (0) absent; (1) present

488 0bu3, M. frontobuccalis posterior: (0) absent; (1) present

489 0bu4, M. tentoriobuccalis lateralis: (0) absent; (1) present.

490 0bu5, M. tentoriobuccalis anterior: (0) absent; (1) present

491 0bu6, M. tentoriobuccalis posterior: (0) absent; (1) present

492 0bux1, “M. frontobuccalis anterior secundus”: (0) absent; (1) present

493 0ph1, M. verticopharyngealis: (0) absent; (1) present. 0ph1 is a very delicate muscle (e.g. 20 µm in diameter in *Dictyophara*) and likely overlooked in older studies?

494 0ph2, M. tentoriopharyngealis: (0) absent; (1) present

495 0ph3, M. postoccipitopharyngealis: (0) absent; (1) present

496 0phx1, “M. sitophori pharyngis”: (0) absent; (1) present

497 0st1, M. annularis stomodaei: (0) with distinctly developed ring muscles; (1) without distinctly developed ring muscles

498 0st2, M. longitudinalis stomodaei: (0) absent; (1) present

499 salivary glands: (0) absent; (1) present

500 number of pairs of salivary glands: (0) 1; (1) 2; (2) 3

502 principal gland (see also Miyamoto 1961): (0) indistinctly bilobate; (1) distinctly bilobate; (2) four lobes; (3) single lobe; (4) multiple lobes; (5) undivided (see also Miles 1972, p. 225)

504 structure of accessory gland (see also Miyamoto 1961): (0) vesicular; (1) tubular

505 distinct bent of accessory salivary duct (see also Miyamoto 1961): (0) absent; (1) present. “Receptacle duct” of *Schizodactylus* (Khattar 1972)

506 structure of principal gland (see also Miyamoto 1961): (0) aciniform; (1) irregular

507 capacity to produce salivary sheaths: (0) absent; (1) present

508 capacity to produce silk or spinning threads (see also Weber 1936): (0) absent; (1) present

510 0hy13, M. annularis salivarii: (0) absent; (1) present

515 protocerebral part folded backwards, above subesophageal ganglion (e.g. Tröster 1990a): (0) absent; (1) present

516 triangular processes of tritocerebrum: (0) absent; (1) present

517 compact complex formed by subesophagial ganglion and brain: (0) absent, (1) present

518 fusion of subesophageal ganglion or subesophageal ganglion-brain-complex with first thoracic ganglion: (0) absent; (1) present

521 bark cell layer ("globuli cells"; see also Graichen 1936): (0) absent; (1) present

522 obturaculum of Stojanovich (1945) (Symmons 1952: "[…] a dense fibrous, cupulate plug of tissue at the back of the head of all Anoplura he examined. It gives support to the origins of muscle of the trophic stylets [...]. It surrounds the sub-esophageal ganglion and separates the head cavity from that of the thorax."; according to von Kéler 1966a an enlarged perlimm as adaptive strengthening element between head and thorax to avoid decapitation during feeding and scratching of the host) (Figs. 22H, 25J): (0) absent; (1) present

523 obturaculum supporting trophic muscles: (0) absent; (1) present

3.4 Character matrix

Table 3: Character states of selected taxa of Acercaria with the outgroups *Oniscigaster*, *Macroxyela*, *Osmylus*, *Schizodactylus*, *Zorotypus*, and *Perla*. Part I of taxon sampling from *Oniscigaster* to *Perissopneumon*. Numbers of characters correspond to those in text, List of potential phylogenetic relevant characters, and List of characters not included in the cladistic analysis. (?) refer to missing character or unclear homology; (-) refer to inapplicable character; (*) refer to taxa not included in cladistic analysis.

	Oniscigaster	*Macroxyela*	*Osmylus*	*Schizodactylus*	*Zorotypus*	*Perla*	*Systelloderes*	*Cryptostemma*	*Hypsipteryx*	Schizopteridae	*Ochterus*	*Corixa*	*Gelastocoris*	*Lethocerus*	*Belostoma*	*Hydrocyrius*	*Nepa*	*Gerris*	*Hydrometra*	*Saldula*	*Triatoma*	*Dysdercus*	*Hackeriella*	*Hemiodoecus*	*Pantinia*	*Peloridium*	*Aphis*	*Macrosiphum*	*Dactylosphaera*	*Trialeurodes*	*Aleurolobus**	*Aleyrodes*	*Psylla*	*Diaphorina*	*Cacopsylla*	*Pseudococcus*	*Perissopneumon*
0	2	2	2	2	2	1	1	1	1	1	2	2	1	1	1	1	1	1	1	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	?	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0
9	0	3	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	?	1	?	0	0	0	0	0	0	0	0	0	0
10	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	?	1	0	0	0	0	0	0
11	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	?	0	0	0	0	0	0	0
12	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	?	0	0	0	0	0	0	0
13	-	-	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	?	-	-	?	-	-	-	-	-	-	-
14	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	?	0	0	0	0	0	0	0
15	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	?	0	0	0	0	0	0	0
16	-	1	-	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	?	-	-	?	-	-	-	-	-	-	-
17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18	1	1	1	0	1	1	1	0	0	-	1	1	1	0	0	0	0	0	0	1	1	0	0	0	0	1	1	1	1	1	1	1	1	1	0	0
19	0	0	0	-	0	0	1	-	-	-	1	1	1	-	-	-	-	-	-	1	1	-	-	-	-	0	0	0	0	1	1	1	0	0	0	-	-
20	0	0	0	0	0	0	0	-	-	-	0	0	0	-	-	-	-	-	-	0	0	-	-	-	-	0	0	0	0	0	0	0	0	0	0	-	-
21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0

	Oniscigaster	*Macroxyela*	*Osmylus*	*Schizodactylus*	*Zorotypus*	*Perla*	*Systelloderes*	*Cryptostemma*	*Hypsipteryx*	Schizopteridae	*Ochterus*	*Corixa*	*Gelastocoris*	*Lethocerus*	*Belostoma*	*Hydrocyrius*	*Nepa*	*Gerris*	*Hydrometra*	*Saldula*	*Triatoma*	*Dysdercus*	*Hackeriella*	*Hemiodoecus*	*Pantinia*	*Peloridium*	*Aphis*	*Macrosiphum*	*Dactylosphaera*	*Trialeurodes*	*Aleurolobus**	*Aleyrodes*	*Psylla*	*Diaphorina*	*Cacopsylla*	*Pseudococcus*	*Perissopneumon*
24	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	3	3
25	?	?	?	?	?	?	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	2	2	2	0	0
31	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
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33	0	-	-	1	-	-	2	2	?	?	1	2	1	1	1	?	?	1	-	1	2	-	-	-	?	?	-	-	-	-	-	-	-	-	-	-
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35	0	-	-	0	0	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	0	-	1	1	1	1	0	0	0	0	0	0	0	0	0	0
36	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
37	1	0	0	0	1	0	-	-	-	-	-	0	-	-	-	-	-	-	-	-	1	-	0	0	0	0	1	1	1	0	0	0	0	0	1	1
38	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
39	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
40	0	0	0	0	0	0	0	1	0	1	1	0	1	1	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
41	0	0	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
42	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
43	-	-	-	-	-	-	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	?	0	1	1
44	1	1	1	1	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1
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46	?	0	1	1	0	1	0	0	0	0	1	0	0	1	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	1	0	0
47	?	0	-	1	0	1	0	0	0	0	1	0	1	1	1	1	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0
48	0	1	0	0	0	1	1	1	1	1	1	0	0	1	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	1	0	0	0	1	1	1	1
49	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
51	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
52	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
53	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
54	0	0	1	1	0	0	1	1	1	1	1	1	-	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

	Oniscigaster	*Macroxyela*	*Osmylus*	*Schizodactylus*	*Zorotypus*	*Perla*	*Systelloderes*	*Cryptostemma*	*Hypsipteryx*	Schizopteridae	*Ochterus*	*Corixa*	*Gelastocoris*	*Lethocerus*	*Belostoma*	*Hydrocyrius*	*Nepa*	*Gerris*	*Hydrometra*	*Saldula*	*Triatoma*	*Dysdercus*	*Hackeriella*	*Hemiodoecus*	*Pantinia*	*Peloridium*	*Aphis*	*Macrosiphum*	*Dactylosphaera*	*Trialeurodes*	*Aleurolobus**	*Aleyrodes*	*Psylla*	*Diaphorina*	*Cacopsylla*	*Pseudococcus*	*Perissopneumon*
55	-	-	0	0	-	-	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
56	-	-	-	-	-	-	1	0	1	0	0	0	0	0	1	0	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1	0	1	0	1	?
57	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
58	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
59	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
60	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
61	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
62	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
63	-	-	-	-	-	-	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1	1	1	1	1
64	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
65	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
66	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
67	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
68	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
69	?	1	?	?	1	1	1	1	?	?	1	1	1	1	?	?	?	1	1	1	?	?	1	1	?	?	0	1	1	0	1	1	0	1	1	1	1
70	?	0	?	?	1	1	1	1	?	?	1	1	1	1	?	?	?	1	1	1	?	?	1	0	?	?	0	1	0	1	0	1	1	0	1	0	1
71	?	1	?	?	1	1	0	0	?	?	0	0	0	0	?	?	?	0	0	0	?	?	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0
72	?	0	?	?	1	0	0	0	?	?	0	0	0	0	?	?	?	0	0	0	?	?	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0
73	?	0	?	?	1	1	0	0	?	?	0	0	0	0	?	0	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0
74	?	0	?	?	1	0	0	0	?	?	0	0	0	0	?	?	?	0	0	0	?	?	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0
75	?	0	?	?	1	0	0	0	?	?	0	0	0	0	?	?	?	0	0	0	?	?	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0
76	?	0	?	?	1	1	1	1	?	?	1	1	1	1	?	?	1	1	1	1	?	?	1	0	?	?	0	1	0	0	0	1	0	1	1	1	1
77	?	1	?	?	0	1	0	0	?	?	0	0	0	0	?	?	?	0	0	0	?	?	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0
78	?	0	?	?	1	1	0	0	?	?	0	0	0	0	?	0	0	0	?	0	0	0	0	0	?	?	0	1	0	1	1	0	0	0	0	1	1
79	?	1	?	?	0	1	1	1	?	?	1	1	1	1	?	?	?	1	1	1	?	?	0	0	?	?	1	0	0	0	0	0	1	0	1	0	0
80	?	0	?	?	0	0	0	0	?	?	0	0	0	0	?	?	?	0	?	0	?	?	1	1	?	?	1	1	1	0	1	1	1	0	1	1	1
81	?	0	?	?	0	0	0	0	?	?	0	0	0	0	?	0	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	1	1	1	1
82	?	0	?	?	0	0	1	1	?	?	1	1	1	1	?	?	?	1	1	0	?	?	0	1	?	?	1	1	0	0	1	1	0	1	1	1	1
83	?	0	?	?	0	0	0	0	?	?	0	0	0	0	?	?	?	0	?	0	?	?	0	1	?	?	1	1	1	1	1	0	1	0	1	0	0
84	?	-	?	?	4	0	0	0	?	?	0	0	0	0	?	?	0	0	0	0	?	?	2	-	?	?	-	1	-	-	-	0	1	-	2	1	1
85	?	0	?	?	0	0	0	0	?	?	0	0	0	0	?	?	?	0	0	0	?	?	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0

	Oniscigaster	*Macroxyela*	*Osmylus*	*Schizodactylus*	*Zorotypus*	*Perla*	*Systelloderes*	*Cryptostemma*	*Hypsipteryx*	Schizopteridae	*Ochterus*	*Corixa*	*Gelastocoris*	*Lethocerus*	*Belostoma*	*Hydrocyrius*	*Nepa*	*Gerris*	*Hydrometra*	*Saldula*	*Triatoma*	*Dysdercus*	*Hackeriella*	*Hemiodoecus*	*Pantinia*	*Peloridium*	*Aphis*	*Macrosiphum*	*Dactylosphaera*	*Trialeurodes*	*Aleurolobus**	*Aleyrodes*	*Psylla*	*Diaphorina*	*Cacopsylla*	*Pseudococcus*	*Perissopneumon*
86	?	1	?	?	1	1	1	1	?	?	1	1	1	1	?	?	?	1	1	1	?	?	1	0	?	?	1	1	1	1	1	0	1	1	0	0
87	?	0	?	?	1	0	0	0	?	?	0	0	0	0	?	?	?	0	0	0	?	?	0	0	?	?	0	0	0	0	0	0	0	0	0	0
88	?	0	?	?	0	0	0	0	?	?	0	0	0	0	?	?	?	0	0	0	?	?	0	0	?	?	0	0	0	0	0	0	0	0	0	0
89	?	1	?	?	0	1	0	0	?	?	0	0	0	0	?	?	?	0	0	0	?	?	0	0	?	?	0	0	0	0	0	0	0	0	0	0
90	?	0	?	?	0	0	0	0	?	?	0	0	0	0	?	?	?	0	0	0	?	?	0	0	?	?	0	0	0	0	0	0	0	0	0	0
91	?	0	?	?	0	0	0	0	?	?	0	0	0	0	?	?	?	0	0	0	?	?	0	0	?	?	0	0	0	0	0	0	0	0	0	0
92	?	0	?	?	0	0	0	0	?	?	0	0	0	0	?	?	?	0	0	0	?	?	0	0	?	?	0	0	0	0	0	0	0	0	0	0
93	?	0	?	?	0	0	0	0	?	?	0	0	0	0	?	?	?	0	0	0	?	?	0	0	?	?	0	0	0	0	0	0	0	0	0	0
94	?	1	?	?	0	0	0	0	?	?	0	0	0	0	?	?	?	0	0	0	?	?	0	0	?	?	0	0	0	0	0	0	0	0	0	0
95	?	0	?	?	0	1	0	0	?	?	0	0	0	0	?	?	?	0	0	0	?	?	0	0	?	?	0	0	0	0	0	0	0	0	0	0
96	?	1	?	?	1	1	1	1	?	?	1	1	1	1	?	?	?	1	1	1	?	?	1	0	?	?	1	0	1	1	0	1	1	0	1	0	0
97	?	0	?	?	0	0	0	0	?	?	0	0	0	0	?	?	?	0	?	0	0	0	0	0	?	?	1	0	0	0	0	0	1	0	0	?
98	?	0	?	0	0	1	0	0	?	?	0	0	0	0	?	?	?	0	0	0	?	?	0	0	?	?	0	0	0	0	0	0	0	0	0	0
99	?	0	?	?	0	0	0	0	?	?	0	0	0	0	?	?	?	0	0	0	?	?	0	0	?	?	0	0	0	0	0	0	0	0	0	0
100	?	0	?	?	1	0	0	0	?	?	0	0	0	0	?	?	?	0	0	0	?	?	0	0	?	?	0	0	0	0	0	0	0	0	0	0
101	0	0	0	0	0	0	0	0	?	?	0	0	0	0	?	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
102	0	0	0	0	0	0	0	0	?	?	0	0	0	0	?	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
103	0	0	0	0	0	0	0	0	?	?	0	0	0	0	?	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
104	0	0	0	0	0	0	0	0	?	?	0	0	0	0	?	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
105	1	1	1	1	1	1	0	0	?	?	0	0	0	0	0	?	1	0	0	1	0	0	1	1	?	?	1	1	1	1	1	1	1	1	1	1
106	0	0	0	0	0	0	-	-	?	?	-	-	-	-	-	?	0	-	-	0	-	-	0	0	?	?	0	0	0	0	0	0	0	0	0	0
107	1	0	1	1	1	1	-	-	?	?	-	-	-	-	-	?	-	-	-	-	-	-	1	1	?	?	1	1	1	1	1	1	1	1	1	1
108	1	1	1	1	1	1	0	0	?	?	0	0	0	0	0	?	0	0	0	0	0	0	1	1	?	?	1	1	1	1	1	1	1	1	1	1
109	1	0	1	0	0	0	-	-	?	?	-	-	-	-	-	?	-	-	-	-	-	-	0	0	?	?	1	1	1	1	1	1	1	0	1	1
110	1	0	0	0	0	0	-	-	?	?	-	-	-	-	-	?	-	-	-	-	-	-	0	0	?	?	0	0	0	0	0	0	0	0	0	0
111	1	1	1	0	1	1	0	0	?	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
112	1	1	1	1	1	1	0	0	?	?	0	0	0	0	0	?	0	0	0	0	0	0	1	1	?	?	1	1	1	1	1	1	1	1	1	1
113	1	1	1	1	1	1	-	-	?	?	-	-	-	-	-	?	-	-	-	-	-	-	1	1	?	?	1	1	1	1	1	1	1	1	1	1
114	0	1	0	0	0	0	-	-	?	?	-	-	-	-	-	?	-	-	-	-	-	-	0	0	?	?	0	0	0	0	0	0	0	0	0	0
115	0	0	0	0	0	0	-	-	?	?	-	-	-	-	-	?	-	-	-	-	-	-	0	0	?	?	0	0	0	0	0	0	0	0	0	0
116	0	0	0	0	0	0	-	-	?	?	-	-	-	-	-	?	-	-	-	-	-	-	0	0	?	?	0	0	0	0	0	0	0	0	0	0

	Oniscigaster	*Macroxyela*	*Osmylus*	*Schizodactylus*	*Zorotypus*	*Perla*	*Systelloderes*	*Cryptostemma*	*Hypsipteryx*	Schizopteridae	*Ochterus*	*Corixa*	*Gelastocoris*	*Lethocerus*	*Belostoma*	*Hydrocyrius*	*Nepa*	*Gerris*	*Hydrometra*	*Saldula*	*Triatoma*	*Dysdercus*	*Hackeriella*	*Hemiodoecus*	*Pantinia*	*Peloridium*	*Aphis*	*Macrosiphum*	*Dactylosphaera*	*Trialeurodes*	*Aleurolobus**	*Aleyrodes*	*Psylla*	*Diaphorina*	*Cacopsylla*	*Pseudococcus*	*Perissopneumon*
117	1	0	0	0	0	0	0	0	?	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
118	0	0	0	0	0	0	-	-	?	?	-	-	-	-	-	?	0	-	-	0	-	-	0	0	?	?	0	0	0	0	0	0	0	0	0	0
119	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0
120	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0
121	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
122	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
123	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
124	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
125	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
126	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	2	2	2	2	0	0	2	0	0	0	0	0	0	0
127	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
128	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-	-	0	0	-	0	0	0	0	0	0	0
129	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
130	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0
131	-	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	?	-	-	-	-
132	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	-	-	-	-	0	0	-	0	0	0	?	0	0	0	0
133	-	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-	-	1	-	2	-	-	-	-	-	-	-	-	-	-	?	-	-	-	-
134	0	0	0	0	0	0	1	0	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	?	0	0	0	0
135	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0
136	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-	-	-	-	0	1	-	-	-	-	-	-	-	-	-	-	?	-	-	-	-
137	0	0	0	0	0	0	1	1	1	1	0	0	1	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0
138	-	-	-	-	-	-	1	2	2	2	-	-	3	-	-	-	-	1	-	0	1	0	-	-	-	-	-	-	-	-	-	-	?	-	-	-	-
139	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	1	1	1	1	1	-	-	-	-	?	0	-	0	0	0	?	0	0	0	0
140	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	?	0	0	0	0
141	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	-	-	-	?	-	-	-	-
142	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0
143	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-	0	0	-	0	0	0	0	0	0	0	0
144	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
145	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-	0	0	-	0	0	0	0	0	0	0	0
146	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-	0	0	-	0	0	0	0	0	0	0	0
147	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	Oniscigaster	*Macroxyela*	*Osmylus*	*Schizodactylus*	*Zorotypus*	*Perla*	*Systelloderes*	*Cryptostemma*	*Hypsipteryx*	Schizopteridae	*Ochterus*	*Corixa*	*Gelastocoris*	*Lethocerus*	*Belostoma*	*Hydrocyrius*	*Nepa*	*Gerris*	*Hydrometra*	*Saldula*	*Triatoma*	*Dysdercus*	*Hackeriella*	*Hemiodoecus*	*Pantinia*	*Peloridium*	*Aphis*	*Macrosiphum*	*Dactylosphaera*	*Trialeurodes*	*Aleurolobus**	*Aleyrodes*	*Psylla*	*Diaphorina*	*Cacopsylla*	*Pseudococcus*	*Perissopneumon*
148	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
149	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
150	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
151	1	1	1	1	1	1	1	1	?	?	1	1	1	1	?	?	?	1	?	1	1	1	1	1	?	?	1	1	1	1	1	1	1	1	1	1
152	1	1	1	1	1	1	1	1	?	?	1	1	1	1	?	?	?	1	?	1	1	1	1	1	?	?	1	1	1	1	1	1	1	1	1	1
153	1	1	0	0	0	?	0	0	?	?	0	0	0	0	?	?	?	0	?	0	0	0	0	0	?	?	1	0	1	0	0	0	0	0	0	0
154	1	1	1	0	1	?	0	0	?	?	0	0	0	0	?	?	?	0	?	0	0	0	0	0	?	?	1	1	1	1	0	1	1	1	1	1
155	6	4	4	0	4	4	1	1	?	?	1	1	1	1	1	1	?	1	1	0	1	1	0	0	?	?	1	0	0	0	0	0	0	0	0	0
156	?	1	1	1	1	?	1	1	?	?	1	1	1	1	?	?	?	1	?	1	?	1	1	1	?	?	?	1	1	?	1	1	?	1	1	1	1
157	?	1	1	1	1	?	1	1	?	?	1	1	1	0	?	?	?	1	?	1	?	1	1	1	?	?	?	1	1	?	1	1	?	1	1	1	1
158	?	0	0	0	0	?	0	0	?	?	0	0	0	0	?	?	?	0	?	0	?	0	0	1	?	?	?	1	0	?	1	0	?	1	0	0	1
159	?	0	0	0	0	?	0	0	?	?	0	0	0	0	?	?	?	0	?	0	?	0	0	1	?	?	?	1	0	?	1	0	?	1	0	0	1
160	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
161	0	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
162	1	1	1	1	1	1	0	0	?	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
163	1	1	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
164	1	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
165	0	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
166	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
167	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
168	4	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
169	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
170	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0
171	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
172	0	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
173	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
174	0	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
175	0	0	0	0	0	0	1	1	?	1	1	1	1	1	1	?	1	1	1	1	1	1	1	?	?	1	1	1	1	1	1	1	1	1	1	1
176	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	?	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0
177	-	-	-	-	-	-	-	-	?	-	-	-	-	-	-	?	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
178	1	1	1	1	1	1	1	1	?	?	0	1	1	1	0	?	1	1	1	1	1	1	0	0	?	?	0	0	1	0	0	0	0	0	0	0

	Oniscigaster	*Macroxyela*	*Osmylus*	*Schizodactylus*	*Zorotypus*	*Perla*	*Systelloderes*	*Cryptostemma*	*Hypsipteryx*	Schizopteridae	*Ochterus*	*Corixa*	*Gelastocoris*	*Lethocerus*	*Belostoma*	*Hydrocyrius*	*Nepa*	*Gerris*	*Hydrometra*	*Saldula*	*Triatoma*	*Dysdercus*	*Hackeriella*	*Hemiodoecus*	*Pantinia*	*Peloridium*	*Aphis*	*Macrosiphum*	*Dactylosphaera*	*Trialeurodes*	*Aleurolobus**	*Aleyrodes*	*Psylla*	*Diaphorina*	*Cacopsylla*	*Pseudococcus*	*Perissopneumon*
179	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
180	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
181	?	?	?	?	?	?	?	?	?	0	?	3	?	?	?	?	?	?	1	2	2	?	?	?	?	?	0	0	?	0	0	0	0	0	0	0
182	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	?	?	?	1	?	?	?	?	?	1	1	?	?	?
183	1	1	0	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
184	0	2	-	4	1	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
185	0	2	-	4	1	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
186	1	1	1	1	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
187	-	-	-	-	-	-	1	1	1	1	1	?	1	1	1	1	1	1	1	1	1	1	0	0	?	?	0	0	0	0	0	0	2	2	2	2	2
188	-	-	-	-	-	-	-	-	-	-	-	?	-	-	-	-	-	-	-	-	-	-	-	-	?	?	-	-	-	-	-	-	0	0	0	1	1
189	0	0	0	0	0	0	1	1	?	?	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?	1	1	1	1	1	1	0	0	0	1	1
190	-	-	-	-	-	-	2	1	?	?	1	0	0	2	2	2	2	3	3	1	0	0	5	5	?	?	4	4	4	5	5	5	-	-	-	6	6
191	0	0	1	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0	?	0	?	?	?	0	?	0	0	?	0	0	?	0	0	?
192	-	-	0	-	-	-	-	-	?	?	-	-	-	-	-	-	-	-	-	-	-	?	-	?	?	?	-	?	-	-	?	-	-	?	-	-	?
193	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?	1	1	?	1	1	1	1	1	1	1	1
194	-	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	?	0	0	0	0	0	0	0	0
195	1	1	1	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
196	1	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
197	1	1	1	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
198	1	0	0	1	0	0	1	0	?	?	0	0	0	0	?	?	0	1	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	1	0
199	0	-	-	0	-	-	1	-	?	?	-	-	-	-	?	?	-	1	-	-	-	-	-	-	?	?	-	-	-	-	-	-	-	-	-	1	-
200	1	0	0	0	0	0	0	0	?	?	0	0	0	0	?	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0
201	1	1	1	1	1	0	0	0	?	?	0	0	0	0	?	?	0	0	0	0	0	0	1	1	?	?	1	1	1	1	1	1	1	1	1	1	1
202	1	0	0	0	0	0	0	0	?	?	0	0	0	0	?	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0
203	1	0	0	0	0	0	0	0	?	?	0	0	0	0	?	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0
204	?	?	?	?	?	?	1	1	?	?	1	0	1	1	?	?	0	1	1	1	1	1	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0
205	?	?	?	?	?	?	0	0	?	?	0	-	0	0	?	?	-	0	0	0	0	0	-	-	?	?	-	-	-	-	-	-	-	-	-	-	-
206	?	?	?	?	?	?	1	1	?	?	1	1	1	1	?	?	1	1	0	1	0	1	1	1	?	?	0	0	0	0	1	0	0	0	1	1	1
207	?	?	?	?	?	?	1	1	?	?	1	0	1	0	?	?	0	1	1	1	1	0	1	1	?	?	0	1	1	0	1	0	1	1	1	0	1
208	?	?	?	?	?	?	1	1	?	?	1	1	1	1	?	?	1	1	0	1	?	1	1	1	?	?	1	1	1	1	1	1	0	0	0	1	1
209	?	?	?	?	?	?	0	0	?	?	0	0	0	0	?	?	0	0	0	0	0	0	1	1	?	?	?	0	0	0	0	0	1	0	1	1	1

	Oniscigaster	*Macroxyela*	*Osmylus*	*Schizodactylus*	*Zorotypus*	*Perla*	*Systelloderes*	*Cryptostemma*	*Hypsipteryx*	Schizopteridae	*Ochterus*	*Corixa*	*Gelastocoris*	*Lethocerus*	*Belostoma*	*Hydrocyrius*	*Nepa*	*Gerris*	*Hydrometra*	*Saldula*	*Triatoma*	*Dysdercus*	*Hackeriella*	*Hemiodoecus*	*Pantinia*	*Peloridium*	*Aphis*	*Macrosiphum*	*Dactylosphaera*	*Trialeurodes*	*Aleurolobus**	*Aleyrodes*	*Psylla*	*Diaphorina*	*Cacopsylla*	*Pseudococcus*	*Perissopneumon*
210	?	?	?	?	?	?	-	-	?	?	-	-	-	-	?	?	-	-	-	-	-	-	1	1	?	?	?	-	-	-	-	-	0	-	0	0	1
211	?	?	?	?	?	?	0	0	?	?	0	0	0	0	?	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
212	0	0	0	0	0	0	0	0	?	?	0	0	0	0	?	?	0	0	0	0	0	0	0	0	?	?	0	0	1	0	0	0	0	0	0	0
213	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
214	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?	1	1	1	1	1	1	1	1	1	1
215	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?	1	1	1	1	1	1	1	1	1	1
216	-	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
217	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	?	0	0	0	0	0	0	0
218	1	1	1	1	0	1	0	0	0	0	1	0	1	1	0	1	1	1	1	0	0	0	0	?	?	?	0	?	?	?	?	?	?	0	?	?	?
219	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	1	1	0	1	0	1	0	?	?	?	1	?	?	?	?	?	?	1	?	?	?
220	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?	1	1	1	1	1	1	1	1	1	1
221	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?	1	1	1	1	1	1	1	1	1	1
222	-	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
223	-	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	?	0	?	?	0	0	0	0	0	0	0	0	0	0
224	-	-	-	-	-	-	1	2	?	?	1	?	1	?	2	?	?	1	-	2	2	2	?	0	?	?	1	2	2	?	2	?	2	?	?	?	2
225	-	-	-	-	-	-	1	1	1	1	1	1	1	1	1	1	1	1	-	1	1	1	?	1	?	?	1	1	1	1	1	1	1	1	1	1	1
226	-	-	-	-	-	-	0	1	?	?	2	0	1	?	1	?	?	2	2	2	2	1	?	2	?	?	1	2	1	?	2	2	1	2	1	?	2
227	0	0	0	0	0	0	1	?	?	?	1	0	1	1	1	1	1	1	1	1	1	0	?	?	?	1	?	?	0	?	?	?	?	?	?	?	?
228	-	-	-	-	-	-	0	?	?	?	0	-	0	0	0	0	0	0	0	0	0	-	?	?	?	?	?	?	-	?	?	?	?	?	?	?	?
229	-	-	-	-	-	-	?	?	?	?	?	-	?	?	?	?	?	?	1	?	1	-	?	?	?	?	?	?	-	?	?	?	?	?	?	?	?
230	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
231	1	0	0	1	1	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
232	0	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
233	0	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
234	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
235	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
236	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
237	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
238	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
239	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	1	0	?	0	0
240	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0

	Oniscigaster	*Macroxyela*	*Osmylus*	*Schizodactylus*	*Zorotypus*	*Perla*	*Systelloderes*	*Cryptostemma*	*Hypsipteryx*	Schizopteridae	*Ochterus*	*Corixa*	*Gelastocoris*	*Lethocerus*	*Belostoma*	*Hydrocyrius*	*Nepa*	*Gerris*	*Hydrometra*	*Saldula*	*Triatoma*	*Dysdercus*	*Hackeriella*	*Hemiodoecus*	*Pantinia*	*Peloridium*	*Aphis*	*Macrosiphum*	*Dactylosphaera*	*Trialeurodes*	*Aleurolobus**	*Aleyrodes*	*Psylla*	*Diaphorina*	*Cacopsylla*	*Pseudococcus*	*Perissopneumon*
241	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	1	0	0	0	0	0	0	0	0
242	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
243	1	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
244	1	1	0	1	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
245	0	0	1	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
246	0	0	1	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
247	1	1	1	1	1	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
248	0	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
249	0	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
250	0	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
251	0	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
252	0	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
253	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
254	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
255	1	3	3	3	3	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
256	0	0	0	0	0	0	1	1	?	?	1	0	1	0	0	0	0	0	0	1	0	1	0	1	?	?	1	1	1	1	1	1	1	1	1	1
257	-	-	-	-	-	-	0	0	?	?	0	-	0	-	-	-	-	-	-	0	-	0	-	1	?	?	1	1	1	1	1	1	1	1	0	0
258	-	-	-	-	-	-	0	0	?	?	0	-	0	-	-	-	-	-	-	0	-	0	-	0	?	?	0	1	1	1	1	0	1	1	0	0	0
259	-	-	-	-	-	-	-	-	?	?	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	?	-	1	0	0	1	-	1	1	-	-	-
260	0	0	?	0	0	1	0	0	?	?	1	1	1	1	1	?	1	1	0	0	0	1	0	0	?	?	0	?	1	0	?	0	0	?	0	0	?
261	1	1	1	1	1	1	0	0	?	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
262	1	1	1	1	1	1	1	1	?	?	1	1	1	1	1	?	1	1	1	1	1	1	1	1	?	?	1	1	1	1	1	1	1	1	1	1
263	2	2	3	4	2	2	2	2	?	?	2	2	2	2	2	?	2	2	2	2	2	2	0	0	?	?	1	1	1	0	1	0	1	1	1	1
264	1	1	1	1	1	1	0	0	?	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
265	1	0	0	1	0	1	0	0	?	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
266	1	1	1	0	1	1	0	0	?	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
267	0	0	0	-	0	0	-	-	?	?	-	-	-	-	-	?	-	-	-	-	-	-	-	-	?	?	-	-	-	-	-	-	-	-	-	-
268	1	1	1	1	1	1	1	1	?	?	1	1	1	1	1	?	1	1	1	1	1	1	1	1	?	?	1	1	1	1	1	1	1	1	1	1
269	0	1	1	1	1	1	0	0	?	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
270	1	1	1	1	1	1	0	0	?	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
271	0	0	0	0	0	0	-	-	?	?	-	-	-	-	-	?	-	-	-	-	-	-	-	-	?	?	-	-	-	-	-	-	-	-	-	-

	Oniscigaster	*Macroxyela*	*Osmylus*	*Schizodactylus*	*Zorotypus*	*Perla*	*Systelloderes*	*Cryptostemma*	*Hypsipteryx*	Schizopteridae	*Ochterus*	*Corixa*	*Gelastocoris*	*Lethocerus*	*Belostoma*	*Hydrocyrius*	*Nepa*	*Gerris*	*Hydrometra*	*Saldula*	*Triatoma*	*Dysdercus*	*Hackeriella*	*Hemiodoecus*	*Pantinia*	*Peloridium*	*Aphis*	*Macrosiphum*	*Dactylosphaera*	*Trialeurodes*	*Aleurolobus**	*Aleyrodes*	*Psylla*	*Diaphorina*	*Cacopsylla*	*Pseudococcus*	*Perissopneumon*
272	1	1	1	1	1	1	0	0	?	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
273	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
274	1	1	1	1	1	1	0	0	?	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
275	0	1	1	1	1	1	0	0	?	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
276	0	0	1	1	1	1	0	0	?	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
277	0	1	1	1	1	1	0	0	?	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
278	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
279	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
280	?	?	?	?	?	?	0	0	?	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	1	1	0	0	0	1	1	0
281	?	?	?	?	?	?	-	-	?	?	-	-	-	-	-	?	-	-	-	-	-	-	-	-	?	?	-	-	0	0	-	-	-	-	0	0	-
282	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
283	?	?	?	?	?	?	0	0	?	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	1	0	0	1	0	0	1	0	0
284	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	1	0	1	0	0	0	0
285	?	0	?	0	0	0	0	0	?	?	1	1	1	1	0	?	0	0	0	0	?	?	1	0	?	?	0	0	0	0	0	0	0	0	0	0
286	1	0	0	0	0	0	0	0	?	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
287	0	0	0	0	0	1	0	0	?	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
288	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
289	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
290	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
291	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
292	-	-	-	-	-	-	2	2	2	-	2	1	2	2	2	2	2	2	2	2	1	1	2	2	2	2	2	2	2	2	2	2	1	2	1	3	2
293	-	-	-	-	-	-	0	0	0	0	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
294	-	-	-	-	-	-	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
295	0	0	0	0	0	0	0	0	?	0	0	0	0	?	0	0	0	0	0	0	1	0	0	0	?	?	0	1	0	0	1	0	0	1	0	0	1
296	-	-	-	-	-	-	0	0	?	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0
297	-	-	-	-	-	-	1	0	?	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	?	?	0	0	0	0	0	0	1	0	0	1	0
298	-	-	-	-	-	-	1	?	0	0	1	1	1	1	1	0	1	1	1	0	1	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0
299	-	-	-	-	-	-	1	1	?	?	1	1	1	1	0	0	?	1	?	1	0	0	0	1	?	?	0	0	0	1	1	1	0	0	0	0	0
300	0	0	0	0	0	0	0	0	?	?	1	?	1	1	1	?	?	1	?	1	0	0	0	0	?	?	0	0	0	0	0	0	?	0	0	0	0
301	1	0	0	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
302	0	-	-	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

	Oniscigaster	*Macroxyela*	*Osmylus*	*Schizodactylus*	*Zorotypus*	*Perla*	*Systelloderes*	*Cryptostemma*	*Hypsipteryx*	Schizopteridae	*Ochterus*	*Corixa*	*Gelastocoris*	*Lethocerus*	*Belostoma*	*Hydrocyrius*	*Nepa*	*Gerris*	*Hydrometra*	*Saldula*	*Triatoma*	*Dysdercus*	*Hackeriella*	*Hemiodoecus*	*Pantinia*	*Peloridium*	*Aphis*	*Macrosiphum*	*Dactylosphaera*	*Trialeurodes*	*Aleurolobus**	*Aleyrodes*	*Psylla*	*Diaphorina*	*Cacopsylla*	*Pseudococcus*	*Perissopneumon*
303	0	-	-	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
304	0	-	-	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
305	1	1	1	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
306	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
307	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
308	0	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
309	0	0	1	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
310	-	-	1	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
311	-	-	1	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
312	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0
313	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
314	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
315	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	?	-	-	-	-	-	-	-	-	-	-
316	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
317	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
318	3	3	3	3	3	3	-	-	-	-	-	-	-	-	-	-	?	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
319	0	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
320	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
321	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
322	1	1	1	1	1	1	0	0	0	?	1'	1	1'	1'	1	1	1	0	0	0	1	1	1	?	1	1	1	0	0	1	0	1	1	1	?	1	0
323	0	0	0	0	0	0	-	-	-	?	0	0	0	0	0	0	0	-	-	-	0	0	1	?	1	1	0	-	-	0	-	0	0	4	?	0	-
324	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	1	1	1	1	1
325	-	-	-	-	-	-	-	-	?	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	?	-	-	-	-	-	-	0	0	0	1	1
326	0	0	0	0	0	0	2	2	2	2	2	?	2	2	2	2	2	2	2	2	2	2	?	?	?	?	3	3	3	3	3	3	4	4	4	0	0
327	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0
328	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	?	-	-	-	-	-	-	-	-	-	-	-
329	0	0	0	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
330	0	0	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
331	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
332	1	1	1	1	1	1	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	0	?	?	?	0	0	?	0	?	0	0	0	?	0
333	0	1	1	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

	Oniscigaster	*Macroxyela*	*Osmylus*	*Schizodactylus*	*Zorotypus*	*Perla*	*Systelloderes*	*Cryptostemma*	*Hypsipteryx*	Schizopteridae	*Ochterus*	*Corixa*	*Gelastocoris*	*Lethocerus*	*Belostoma*	*Hydrocyrius*	*Nepa*	*Gerris*	*Hydrometra*	*Saldula*	*Triatoma*	*Dysdercus*	*Hackeriella*	*Hemiodoecus*	*Pantinia*	*Peloridium*	*Aphis*	*Macrosiphum*	*Dactylosphaera*	*Trialeurodes*	*Aleurolobus**	*Aleyrodes*	*Psylla*	*Diaphorina*	*Cacopsylla*	*Pseudococcus*	*Perissopneumon*
334	-	0	0	0	-	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
335	-	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
336	1	1	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
337	1	1	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
338	0	0	1	1	1	0	0	0	?	?	0	0	0	0	?	?	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
339	1	1	1	1	1	0	0	0	?	?	0	0	0	0	?	?	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
340	1	0	1	1	0	0	0	0	?	?	0	0	0	0	?	?	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
341	1	1	1	1	1	0	0	0	?	?	0	0	0	0	?	?	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
342	?	?	?	?	?	?	1	1	?	?	1	1	1	1	?	?	1	1	?	1	0	0	1	0	?	?	1	0	0	1	0	1	0	0	1	0
343	?	?	?	?	?	?	1	1	?	?	1	1	1	1	?	?	1	1	?	1	?	?	0	1	?	?	1	0	0	1	1	1	0	0	1	0
344	?	?	?	?	?	?	1	1	?	?	1	1	1	1	?	?	1	1	?	1	?	?	-	0	?	?	1	-	-	0	0	1	-	-	-	1	-
345	?	?	?	?	?	?	1	1	?	?	1	1	1	1	?	?	1	1	?	1	1	?	1	1	?	?	1	1	0	1	0	0	1	0	1	1
346	?	?	?	?	?	?	1	1	?	?	1	0	1	1	?	?	1	1	?	1	1	1	1	1	?	?	1	1	1	1	1	1	0	0	1	0
347	?	?	?	?	?	?	0	0	?	?	0	0	0	0	?	?	0	0	?	0	0	0	0	0	?	?	1	0	1	0	1	0	0	0	0	1
348	?	?	?	?	?	?	0	0	?	?	0	0	0	0	?	?	0	0	?	0	0	0	0	0	?	?	1	0	1	0	0	0	0	0	0	0
349	?	?	?	?	?	?	1	1	?	?	1	?	1	1	?	?	1	1	?	1	1	1	1	1	?	?	1	1	1	1	1	1	1	1	1	1
350	?	?	?	?	?	?	0	0	?	?	0	0	0	0	?	?	0	0	?	0	0	0	0	0	?	?	1	0	1	0	0	0	0	0	0	0
351	?	?	?	?	?	?	1	1	?	?	1	1	1	1	?	?	1	1	?	1	0	1	0	0	?	?	1	1	1	0	1	1	0	1	0	1	0
352	?	?	?	?	?	?	1	1	?	?	1	0	1	1	?	?	1	1	?	1	1	1	1	1	?	?	1	1	1	1	1	1	0	0	1	0	0
353	0	0	0	0	0	0	0	0	?	?	0	0	0	0	?	?	0	0	?	0	0	0	0	0	?	?	1	0	1	0	0	0	0	0	1	1
354	0	0	0	0	0	0	0	0	?	?	0	0	0	0	?	?	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	1	1	1	1
355	0	0	0	0	0	0	0	0	?	?	0	0	0	0	?	?	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	1	1
356	?	?	?	?	?	?	1	1	?	?	1	?	0	1	?	?	1	1	?	1	1	1	1	0	?	?	1	0	0	1	0	1	0	0	1	0
357	?	?	?	?	?	?	0	1	?	?	0	?	-	0	?	?	0	0	?	0	0	0	2	-	?	?	1	-	-	0	-	0	-	-	-	1	-
358	?	?	?	?	?	?	0	0	?	?	0	0	0	1	?	?	?	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
359	?	?	?	?	?	?	0	0	?	?	0	0	0	0	?	?	0	0	?	0	0	0	0	0	?	?	0	0	1	0	0	0	0	0	0	0
360	0	0	0	0	0	0	0	0	?	?	0	0	0	0	?	?	0	0	?	0	0	0	0	0	?	?	1	1	1	1	1	0	1	0	1	0	0
361	?	?	?	?	?	?	0	0	?	?	0	0	0	0	?	?	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	1	0	1	1
362	0	0	0	0	0	0	0	0	?	?	0	0	0	0	?	?	0	0	?	0	0	0	0	0	?	?	0	1	0	1	0	0	0	1	1	0	1
363	0	0	0	0	0	0	0	0	?	?	0	0	0	0	?	?	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	1
364	1	1	0	0	1	0	0	0	?	?	0	0	0	0	?	?	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0

	Oniscigaster	*Macroxyela*	*Osmylus*	*Schizodactylus*	*Zorotypus*	*Perla*	*Systelloderes*	*Cryptostemma*	*Hypsipteryx*	Schizopteridae	*Ochterus*	*Corixa*	*Gelastocoris*	*Lethocerus*	*Belostoma*	*Hydrocyrius*	*Nepa*	*Gerris*	*Hydrometra*	*Saldula*	*Triatoma*	*Dysdercus*	*Hackeriella*	*Hemiodoecus*	*Pantinia*	*Peloridium*	*Aphis*	*Macrosiphum*	*Dactylosphaera*	*Trialeurodes*	*Aleurolobus**	*Aleyrodes*	*Psylla*	*Diaphorina*	*Cacopsylla*	*Pseudococcus*	*Perissopneumon*
365	1	0	0	0	0	0	0	0	?	?	0	0	0	0	?	?	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
366	?	?	?	?	?	?	0	0	?	?	0	0	0	0	?	?	0	0	?	0	0	0	0	0	?	?	0	0	0	1	0	0	1	0	0	1
367	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
368	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
369	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
370	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
371	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
372	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
373	1	0	1	1	1	1	0	0	?	?	0	0	0	0	?	0	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
374	0	-	0	0	0	0	-	-	?	?	-	-	-	-	?	-	-	-	?	-	-	-	-	-	?	?	-	-	-	-	-	-	-	-	-	-
375	1	1	1	1	1	1	0	0	?	?	0	0	0	0	?	0	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
376	0	0	0	0	0	0	-	-	?	?	-	-	-	-	?	?	-	-	?	-	-	-	-	-	?	?	-	-	-	-	-	-	-	-	-	-
377	0	0	0	0	0	0	-	-	?	?	-	-	-	-	?	?	-	-	?	-	-	-	-	-	?	?	-	-	-	-	-	-	-	-	-	-
378	1	1	0	1	1	1	0	0	?	?	0	0	0	0	?	0	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
379	3	2	-	3	2	0	-	-	?	?	-	-	-	-	?	?	-	-	?	-	-	-	-	-	?	?	-	-	-	-	-	-	-	-	-	-
380	0	1	0	0	0	0	0	0	?	?	0	0	0	0	?	?	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
381	0	0	0	0	0	0	0	0	?	?	0	0	0	0	?	0	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
382	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	?	1	1	1	1	1	1	1	1	?	?	1	1	1	1	1	1	1	1	1	1
383	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
384	0	1	0	0	1	0	1	1	1	1	1	1	1	1	1	?	1	1	1	1	1	1	1	1	?	?	1	1	1	1	1	1	1	1	1	1
385	-	0	-	-	0	-	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
386	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
387	-	0	-	-	0	-	1	1	1	1	1	1	1	1	1	?	1	1	1	1	1	1	1	1	?	?	1	1	1	1	1	1	1	1	1	1
388	0	0	0	0	0	1	1	1	1	1	1	0	1	1	1	?	1	1	1	1	1	1	0	0	?	?	0	0	0	0	0	0	0	0	0	0
389	-	1	1	1	1	1	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
390	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
391	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
392	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	?	1	1	1	1	1	1	1	1	?	?	1	1	1	1	1	1	1	1	1	1
393	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	1	1	1	1	1	1	1	?	?	1	1	1	1	1	1	1	1	1	1
394	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
395	-	0	0	0	0	0	-	-	-	-	-	-	-	-	-	?	-	-	-	-	-	-	-	-	?	?	-	-	-	-	-	-	-	-	-	-

	Oniscigaster	*Macroxyela*	*Osmylus*	*Schizodactylus*	*Zorotypus*	*Perla*	*Systelloderes*	*Cryptostemma*	*Hypsipteryx*	Schizopteridae	*Ochterus*	*Corixa*	*Gelastocoris*	*Lethocerus*	*Belostoma*	*Hydrocyrius*	*Nepa*	*Gerris*	*Hydrometra*	*Saldula*	*Triatoma*	*Dysdercus*	*Hackeriella*	*Hemiodoecus*	*Pantinia*	*Peloridium*	*Aphis*	*Macrosiphum*	*Dactylosphaera*	*Trialeurodes*	*Aleurolobus**	*Aleyrodes*	*Psylla*	*Diaphorina*	*Cacopsylla*	*Pseudococcus*	*Perissopneumon*
396	-	0	?	0	0	0	-	-	-	-	-	-	-	-	-	?	-	-	-	-	-	-	-	-	?	?	-	-	-	-	-	-	-	-	-	-
397	-	0	0	?	0	0	-	-	-	-	-	-	-	-	-	?	-	-	-	-	-	-	-	-	?	?	-	-	-	-	-	-	-	-	-	-
398	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
399	-	0	-	0	-	0	-	-	-	-	-	-	-	-	-	?	-	-	-	-	-	-	-	-	?	?	-	-	-	-	-	-	-	-	-	-
400	-	?	-	0	-	0	-	-	-	-	-	-	-	-	-	?	-	-	-	-	-	-	-	-	?	?	-	-	-	-	-	-	-	-	-	-
401	-	?	-	-	-	-	-	-	-	-	-	-	-	-	-	?	-	-	-	-	-	-	-	-	?	?	-	-	-	-	-	-	-	-	-	-
402	-	0	-	0	-	0	-	-	-	-	-	-	-	-	-	?	-	-	-	-	-	-	-	-	?	?	-	-	-	-	-	-	-	-	-	-
403	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
404	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
405	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	-	-	-	-	-	-	-	-	?	?	-	-	-	-	-	-	-	-	-	-
406	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	-	-	-	-	-	-	-	-	?	?	-	-	-	-	-	-	-	-	-	-
407	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
408	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	-	-	-	-	-	-	-	-	?	?	-	-	-	-	-	-	-	-	-	-
409	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	?	1	1	1	1	1	1	1	1	?	?	1	1	1	1	1	1	1	1	1	1
410	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
411	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
412	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
413	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
414	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	-	-	-	-	-	-	-	-	?	?	-	-	-	-	-	-	-	-	-	-
415	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
416	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	-	-	-	-	-	-	-	-	?	?	-	-	-	-	-	-	-	-	-	-
417	0	0	0	0	0	0	-	-	?	?	-	-	-	-	-	?	-	-	-	-	-	-	1	1	?	?	0	0	1	?	1	1	1	1	0	0
418	0	0	0	0	0	0	?	?	?	?	1	1	0	1	1	?	?	3	0	0	3	1	?	?	?	?	?	?	1	0	?	?	0	?	?	?	?
419	0	0	0	0	0	0	1	1	?	?	1	1	1	1	1	?	1	1	1	1	1	1	1	1	?	?	1	1	1	1	1	1	1	1	1	1
420	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
421	-	0	-	-	0	-	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
422	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
423	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
424	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
425	0	0	0	0	0	0	0	0	?	?	0	0	0	0	?	?	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
426	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	?	?	?	0	?	0	0	?	0	?	?	0	0	?

	Oniscigaster	*Macroxyela*	*Osmylus*	*Schizodactylus*	*Zorotypus*	*Perla*	*Systelloderes*	*Cryptostemma*	*Hypsipteryx*	Schizopteridae	*Ochterus*	*Corixa*	*Gelastocoris*	*Lethocerus*	*Belostoma*	*Hydrocyrius*	*Nepa*	*Gerris*	*Hydrometra*	*Saldula*	*Triatoma*	*Dysdercus*	*Hackeriella*	*Hemiodoecus*	*Pantinia*	*Peloridium*	*Aphis*	*Macrosiphum*	*Dactylosphaera*	*Trialeurodes*	*Aleurolobus**	*Aleyrodes*	*Psylla*	*Diaphorina*	*Cacopsylla*	*Pseudococcus*	*Perissopneumon*
427	1	1	1	1	1	1	0	0	?	?	0	0	0	0	?	?	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
428	0	0	0	0	0	0	-	-	?	?	-	-	-	-	?	?	-	-	?	-	-	-	-	-	?	?	-	-	-	-	-	-	-	-	-	-
429	1	0	1	0	1	0	0	0	?	?	0	0	0	0	?	?	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
430	1	-	0	-	1	-	-	-	?	?	-	-	-	-	?	?	-	-	?	-	-	-	-	-	?	?	-	-	-	-	-	-	-	-	-	-
431	1	0	0	0	0	1	0	0	?	?	0	0	0	0	?	?	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
432	0	0	0	1	?	0	0	0	?	?	0	0	0	0	?	?	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
433	-	-	-	0	?	-	-	-	?	?	-	-	-	-	?	?	-	-	?	-	-	-	-	-	?	?	-	-	-	-	-	-	-	-	-	-
434	-	-	-	0	?	-	-	-	?	?	-	-	-	-	?	?	-	-	?	-	-	-	-	-	?	?	-	-	-	-	-	-	-	-	-	-
435	0	1	1	0	1	1	0	0	?	?	0	0	0	0	?	?	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
436	0	1	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
437	1	1	1	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
438	0	1	1	0	1	0	0	0	?	?	0	0	0	0	?	?	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
439	1	0	0	0	0	0	0	0	?	?	0	0	0	0	?	?	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
440	0	1	1	1	1	1	1	1	?	?	1	1	1	1	1	?	1	1	1	1	1	1	1	1	?	?	1	1	1	1	1	1	1	1	1	1
441	-	1	1	1	1	1	0	1	?	?	1	1	1	1	1	?	1	1	0	1	1	1	1	1	?	?	1	1	1	2	1	1	2	1	2	1	1
442	0	0	0	0	0	0	0	0	?	?	0	?	0	0	?	?	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
443	0	0	0	0	0	0	0	0	?	?	0	0	0	0	?	?	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
444	-	-	-	-	-	-	-	-	?	?	-	-	-	-	?	?	-	-	?	-	-	-	-	-	?	?	-	-	-	-	-	-	-	-	-	-
445	0	0	0	0	0	0	0	0	?	?	0	0	0	0	?	0	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
446	0	0	0	0	0	0	0	0	?	?	0	0	0	0	?	?	?	0	?	0	0	0	1	0	?	?	1	0	1	1	0	1	1	0	1	0	0
447	0	0	0	0	0	0	0	0	?	?	0	0	0	0	?	0	0	0	?	0	0	0	0	0	?	?	1	0	1	0	0	0	0	0	0	0
448	0	0	0	0	0	0	0	0	?	?	0	0	0	0	?	0	0	0	?	0	0	0	0	0	?	?	1	0	0	0	0	0	0	0	0	0
449	0	0	0	0	0	0	0	0	?	?	0	0	0	0	?	0	0	0	?	0	0	0	0	0	?	?	1	0	1	0	0	0	0	0	0	0
450	0	0	0	0	0	0	0	0	?	?	0	0	0	0	?	0	0	0	?	0	0	0	0	0	?	?	1	0	0	0	0	0	0	0	0	0
451	0	0	1	0	0	0	0	0	?	?	0	0	0	0	?	?	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
452	0	0	0	1	0	0	1	1	?	?	1	1	?	1	1	?	?	1	?	1	1	1	0	?	?	?	1	?	?	1	?	1	1	?	1	?	?
453	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
454	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
455	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	?	-	-	-	-	-	-	-	-	-	-
456	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	?	-	-	-	-	-	-	-	-	-	-
457	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0

	Oniscigaster	*Macroxyela*	*Osmylus*	*Schizodactylus*	*Zorotypus*	*Perla*	*Systelloderes*	*Cryptostemma*	*Hypsipteryx*	Schizopteridae	*Ochterus*	*Corixa*	*Gelastocoris*	*Lethocerus*	*Belostoma*	*Hydrocyrius*	*Nepa*	*Gerris*	*Hydrometra*	*Saldula*	*Triatoma*	*Dysdercus*	*Hackeriella*	*Hemiodoecus*	*Pantinia*	*Peloridium*	*Aphis*	*Macrosiphum*	*Dactylosphaera*	*Trialeurodes*	*Aleurolobus**	*Aleyrodes*	*Psylla*	*Diaphorina*	*Cacopsylla*	*Pseudococcus*	*Perissopneumon*
458	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0
459	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	?	-	-	-	-	-	-	-	-	-	-	-
460	0	0	0	0	0	0	?	?	?	?	0	0	0	0	1	?	?	0	?	0	0	?	?	?	?	?	1	1	1	1	1	?	1	1	1	1	1
461	-	-	-	-	-	-	?	?	?	?	-	-	-	-	0	?	?	-	?	-	-	?	?	?	?	?	0	0	0	?	?	?	1	1	1	?	?
462	-	-	-	-	-	-	?	?	?	?	-	-	-	-	0	?	?	-	?	-	-	?	?	?	?	?	0	0	0	?	?	?	0	0	0	?	?
463	-	-	-	?	-	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	-	?	?	?	0	0	0	?	?	?	1	1	1	?	?
464	-	-	-	?	-	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	-	?	?	?	0	0	0	?	?	?	1	1	1	?	?
465	-	-	-	?	-	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	-	?	?	?	1	1	1	?	?	?	1	1	1	?	?
466	-	-	-	?	-	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	?	?	?	1	1	1	?	?
467	-	-	-	?	-	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	-	?	?	?	0	0	0	?	?	?	1	1	1	?	?
468	0	0	0	0	0	0	1	1	?	?	0	1	?	1	?	?	?	1	?	1	1	?	1	?	?	?	1	1	1	1	?	?	1	1	1	0	?
469	-	-	-	-	-	-	1	1	?	?	-	1	?	1	?	?	?	1	?	1	1	?	1	?	?	?	0	0	0	1	?	?	1	1	1	-	?
470	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
471	0	0	0	0	0	0	0	0	?	?	1	1	1	1	1	?	1	0	0	1	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0
472	1	1	0	1	1	1	0	0	?	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0
473	2	2	2	2	2	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0	0	1	?	?	?	1	?	1	1	?	1	1	?	1	1	?
474	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?	1	1	1	1	1	1	1	1	1	1	1
475	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0
476	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0
477	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	?	-	-	-	-	-	-	-	-	-	-	-
478	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0
479	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0
480	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0
481	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0
482	0	0	0	0	0	0	0	0	?	?	0	0	?	?	?	?	0	0	?	?	0	?	0	?	?	?	0	?	0	0	?	0	0	?	0	0	?
483	1	1	1	1	1	0	0	0	?	?	0	1	?	0	0	?	0	0	0	0	0	0	1	1	?	?	1	1	1	1	1	1	1	1	1	1	1
484	1	1	0	1	1	1	0	0	?	?	0	0	?	?	?	?	0	0	?	?	0	?	0	?	?	?	0	?	0	0	?	0	0	?	0	0	?
485	1	1	1	1	1	1	1	1	?	?	1	1	1	1	?	?	1	1	?	1	1	0	1	1	?	?	1	1	1	1	1	1	1	1	1	1	1
486	1	1	1	1	?	0	1	1	?	?	1	1	1	1	?	?	1	1	?	0	1	1	1	1	?	?	1	1	1	1	1	1	1	1	1	1	1
487	1	1	1	1	1	1	1	1	?	?	1	1	1	1	?	?	1	1	?	1	1	1	1	1	?	?	1	1	1	1	1	1	1	1	1	1	1
488	1	1	1	1	1	1	1	1	?	?	1	1	1	1	?	?	1	1	?	1	1	1	1	0	?	?	0	0	1	?	0	1	?	0	1	1	1

	Oniscigaster	*Macroxyela*	*Osmylus*	*Schizodactylus*	*Zorotypus*	*Perla*	*Systelloderes*	*Cryptostemma*	*Hypsipteryx*	Schizopteridae	*Ochterus*	*Corixa*	*Gelastocoris*	*Lethocerus*	*Belostoma*	*Hydrocyrius*	*Nepa*	*Gerris*	*Hydrometra*	*Saldula*	*Triatoma*	*Dysdercus*	*Hackeriella*	*Hemiodoecus*	*Pantinia*	*Peloridium*	*Aphis*	*Macrosiphum*	*Dactylosphaera*	*Trialeurodes*	*Aleurolobus**	*Aleyrodes*	*Psylla*	*Diaphorina*	*Cacopsylla*	*Pseudococcus*	*Perissopneumon*
489	1	0	0	0	0	0	0	0	?	?	0	0	0	0	?	?	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
490	0	0	1	1	0	0	0	0	?	?	1	1	1	1	?	?	?	0	?	1	0	?	1	0	?	?	1	0	1	0	0	0	1	0	1	1	0
491	1	0	1	1	1	0	0	0	?	?	0	0	0	0	?	?	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0
492	0	0	0	1	0	0	0	0	?	?	0	0	0	0	?	0	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0
493	1	1	1	1	1	0	0	0	?	?	1	1	1	1	?	?	?	0	?	1	1	?	1	0	?	?	0	0	0	0	0	0	0	1	0	1	0
494	0	1	1	1	1	0	0	0	?	?	0	0	0	0	?	?	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	1	0	0	0
495	0	0	0	0	0	0	0	0	?	?	0	0	0	0	?	?	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0
496	0	0	0	0	0	0	0	0	?	?	0	0	0	0	?	?	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0
497	0	1	0	0	0	0	0	0	?	?	0	0	?	?	?	?	0	0	?	?	0	?	1	?	?	?	1	?	1	0	?	1	1	?	0	0	?
498	1	1	0	1	1	0	0	0	?	?	0	0	?	?	?	?	0	0	?	?	0	?	0	?	?	?	0	?	0	0	?	0	0	?	0	0	?
499	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?	?	1	?	1	1	?	1	1	?	1	1	?
500	-	0	2	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?	?	1	?	1	1	?	1	1	?	1	1	?
501	-	?	?	1	?	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?	?	1	?	1	1	?	1	1	?	1	1	?
502	-	?	?	4	?	5	0	0	0	0	1	1	1	1	1	1	1	1	1	3	1	2	0	?	?	?	0	?	1	0	?	0	?	?	4	4	?
503	-	?	?	1	?	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?	?	1	?	1	1	?	1	?	?	1	1	?
504	-	?	?	1	?	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	?	?	?	0	?	0	0	?	0	?	?	0	0	?
505	-	?	?	0	?	0	1	?	?	?	?	1	?	1	?	?	1	1	1	1	1	1	1	?	?	?	0	?	1	0	?	0	?	?	0	?	?
506	-	?	?	0	?	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	?	?	?	0	?	0	1	?	1	?	?	0	0	?
507	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	?	?	?	?	1	1	1	1	1	1	1	1	1	1	1
508	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
509	0	?	?	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	?	0	0	?	0	?	?	0	0	?
510	0	1	0	0	1	0	0	0	?	?	0	0	0	0	?	?	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0
511	0	0	0	0	0	0	0	0	?	?	0	0	0	0	?	?	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0
512	0	0	0	0	0	0	0	0	?	?	0	0	0	0	?	?	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0
513	0	0	0	1	0	0	0	0	?	?	0	0	0	0	?	?	0	0	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0
514	1	1	1	1	1	1	1	1	?	1	?	1	1	1	?	?	1	1	1	?	?	?	1	?	?	?	1	?	1	1	?	1	1	?	1	1	?
515	0	0	0	0	1	1	1	1	?	0	?	0	0	0	?	?	0	0	0	?	?	?	0	?	?	?	0	?	0	0	?	0	0	?	0	0	?
516	0	0	0	0	0	0	0	0	?	0	?	0	1	0	?	?	0	0	0	?	?	0	1	?	?	?	0	?	0	0	?	0	0	?	0	1	?
517	0	0	0	0	0	0	1	1	?	1	?	0	1	0	?	?	1	1	1	?	?	1	0	?	?	?	0	?	0	0	?	0	0	?	0	0	?
518	0	0	0	0	0	0	0	0	?	0	?	1	0	1	?	?	1	1	0	?	?	?	1	?	?	?	0	?	0	0	?	0	0	?	1	0	?
519	0	0	0	0	0	0	0	1	?	1	?	0	0	0	?	?	0	1	1	?	0	0	1	?	?	?	0	0	0	1	0	1	1	0	1	1	0

	Oniscigaster	*Macroxyela*	*Osmylus*	*Schizodactylus*	*Zorotypus*	*Perla*	*Systelloderes*	*Cryptostemma*	*Hypsipteryx*	Schizopteridae	*Ochterus*	*Corixa*	*Gelastocoris*	*Lethocerus*	*Belostoma*	*Hydrocyrius*	*Nepa*	*Gerris*	*Hydrometra*	*Saldula*	*Triatoma*	*Dysdercus*	*Hackeriella*	*Hemiodoecus*	*Pantinia*	*Peloridium*	*Aphis*	*Macrosiphum*	*Dactylosphaera*	*Trialeurodes*	*Aleurolobus**	*Aleyrodes*	*Psylla*	*Diaphorina*	*Cacopsylla*	*Pseudococcus*	*Perissopneumon*
520	1	1	1	0	1	0	1	1	?	1	?	0	0	0	?	?	0	1	1	?	1	?	1	?	?	?	1	1	1	1	1	1	1	1	1	1
521	1	1	1	?	1	?	1	1	?	?	?	1	1	?	?	?	?	1	?	?	?	?	?	0	?	?	?	?	?	1	1	?	1	1	?	1	0	?
522	0	0	0	0	0	0	0	0	?	0	?	0	0	0	?	?	0	0	0	?	?	0	0	?	?	?	?	0	?	0	0	?	0	0	?	0	0	?
523	-	-	-	-	-	-	-	-	?	-	?	-	-	-	?	?	-	-	-	?	?	-	-	?	?	?	-	?	-	-	?	-	-	?	-	-	?

Table 3: Character states of selected taxa of Acercaria with the outgroups *Oniscigaster*, *Macroxyela*, *Osmylus*, *Schizodactylus*, *Zorotypus*, and *Perla*. Part II of taxon sampling from *Tibicina* to *Haematomyzus*. Numbers of characters correspond to those in text, List of potential phylogenetic relevant characters, and List of characters not included in the cladistic analysis. (?) refer to missing character or unclear homology; (-) refer to inapplicable character; (*) refer to taxa not included in cladistic analysis.

	Tibicina	*Idiocerus*	*Philaenus*	*Lepyronia*	*Platypleura*	*Oxyrhachis*	*Scolops*	*Melicharia**	*Dictyophara*	*Aeolothrips f.*	*Aeolothrips i.*	*Thrips*	*Haplothrips*	*Phlaeothrips*	*Psocus*	*Psococerastis*	*Stenopsocus*	*Caecilius*	*Cerobasis*	*Troctes*	*Liposcelis*	*Gliricola*	*Myrsidea*	*Pseudomenopon*	*Piagetiella*	*Trochiloecetes*	*Trimenopon*	*Bovicola*	*Ornithobius*	*Columbicola*	*Haematopinus*	*Hybophthirus*	*Pediculus*	*Phthirus*	*Haematomyzus*
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	2	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1
2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
4	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	2	2	0	0	0	0	0	0	0	0	0	0
10	1	0	0	0	1	0	0	0	0	1	1	1	1	1	1	?	1	1	1	?	?	?	0	?	1	?	1	0	?	0	0	1	0	?	1
11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	?	1	1	0	?	?	?	1	?	0	?	?	0	?	0	0	?	0	?	?

	Tibicina	*Idiocerus*	*Philaenus*	*Lepyronia*	*Platypleura*	*Oxyrhachis*	*Scolops*	*Melicharia**	*Dictyophara*	*Aeolothrips f.*	*Aeolothrips i.*	*Thrips*	*Haplothrips*	*Phlaeothrips*	*Psocus*	*Psococerastis*	*Stenopsocus*	*Caecilius*	*Cerobasis*	*Troctes*	*Liposcelis*	*Gliricola*	*Myrsidea*	*Pseudomenopon*	*Piagetiella*	*Trochiloecetes*	*Trimenopon*	*Bovicola*	*Ornithobius*	*Columbicola*	*Haematopinus*	*Hybophthirus*	*Pediculus*	*Phthirus*	*Haematomyzus*
12	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	?	?	?	0	?	0	?	1	0	?	0	0	0	0	?	0
13	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	-	-	-	?	?	?	-	?	-	?	0	-	?	-	-	-	-	?	-
14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	?	?	?	0	?	0	?	0	0	?	0	0	0	0	?	0
15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	?	?	?	0	?	0	?	0	0	?	0	0	0	0	?	0
16	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	?	0	0	-	?	?	?	-	?	-	?	-	-	?	-	-	-	-	?	-
17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
18	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19	0	1	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
20	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0
22	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1
23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0
24	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	2	2	2	2	2	2	2	2	3	-	3	3	3	3
25	0	0	0	0	0	0	?	?	?	1	1	1	0	0	0	0	0	0	0	0	0	1	1	?	1	1	1	1	?	1	?	-	1	?	?
26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	-	0	?	0	0
27	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0	1	1	1	-	1	?	1	1
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0
31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	0
32	0	1	0	0	0	1	0	1	0	1	1	0	0	1	1	1	0	0	1	?	0	0	0	0	0	0	1	0	0	1	1	1	1	?	1
33	-	2	-	-	-	2	-	2	-	2	2	-	-	2	2	2	-	-	2	?	-	-	-	-	-	-	2	-	-	1	0	0	0	?	1
34	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0
35	2	2	2	2	2	2	3	3	3	0	0	0	0	0	3	3	3	3	3	-	3	-	-	-	-	-	-	-	-	0	-	-	-	-	-
36	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
37	1	1	1	0	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
38	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
39	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
41	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1
42	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	Tibicina	*Idiocerus*	*Philaenus*	*Lepyronia*	*Platypleura*	*Oxyrhachis*	*Scolops*	*Melicharia**	*Dictyophara*	*Aeolothrips f.*	*Aeolothrips i.*	*Thrips*	*Haplothrips*	*Phlaeothrips*	*Psocus*	*Psococerastis*	*Stenopsocus*	*Caecilius*	*Cerobasis*	*Troctes*	*Liposcelis*	*Gliricola*	*Myrsidea*	*Pseudomenopon*	*Piagetiella*	*Trochiloecetes*	*Trimenopon*	*Bovicola*	*Ornithobius*	*Columbicola*	*Haematopinus*	*Hybophthirus*	*Pediculus*	*Phthirus*	*Haematomyzus*
43	1	1	1	1	1	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
44	1	1	1	?	1	1	0	1	0	1	1	1	1	1	1	1	1	1	1	?	0	1	1	0	1	1	1	1	1	1	0	1	0	0	0
45	1	1	1	?	1	1	?	1	1	1	1	0	0	0	1	1	1	1	1	?	1	1	1	1	1	1	1	1	1	1	0	1	0	0	1
46	1	1	0	0	1	0	0	1	0	0	0	0	0	0	1	1	1	1	1	?	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1
47	1	0	0	0	1	0	0	1	0	0	0	0	0	0	1	1	1	1	1	?	1	0	0	0	0	1	1	1	1	1	1	1	1	1	1
48	1	0	0	0	1	1	1	1	1	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	1	0	0	1	0	0	1	1	0
49	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0
51	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	0	1	1	-	-	-	-	-
52	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	?	1	-	-	-	-	-
53	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	0	1	0	-	-	-	-	-
54	1	1	1	1	1	1	1	-	1	1	1	1	0	0	1	1	1	1	1	?	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0
55	0	0	0	0	0	0	0	-	0	1	1	1	-	-	0	0	0	0	0	?	0	-	0	-	-	0	-	-	-	-	-	-	-	-	-
56	1	1	1	1	1	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
57	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
58	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	1	1	0	0	0
59	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
60	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
61	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
62	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
63	0	1	0	1	0	0	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
64	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0
65	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	1	1
66	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0
67	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0
68	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
69	?	?	1	?	1	1	?	1	1	?	1	1	1	1	?	?	1	1	1	?	1	?	1	?	1	?	1	?	1	1	?	1	1	1	1	?	1
70	?	?	1	?	1	1	?	1	1	?	1	1	1	1	?	?	1	1	1	?	0	?	1	?	1	?	1	0	?	0	0	0	0	?	?
71	?	?	0	?	0	0	?	0	0	?	0	0	0	0	?	?	0	0	0	?	0	?	0	?	0	?	0	0	?	0	0	0	0	?	0
72	?	?	0	?	0	0	?	0	0	?	0	0	0	0	?	?	0	0	0	?	0	?	0	?	0	?	0	0	?	0	0	0	0	?	0
73	?	?	0	?	0	0	?	0	0	?	1	0	1	1	?	?	1	1	0	?	0	?	0	?	0	?	0	0	?	0	0	0	0	?	0

	Tibicina	*Idiocerus*	*Philaenus*	*Lepyronia*	*Platypleura*	*Oxyrhachis*	*Scolops*	*Melicharia**	*Dictyophara*	*Aeolothrips f.*	*Aeolothrips i.*	*Thrips*	*Haplothrips*	*Phlaeothrips*	*Psocus*	*Psococerastis*	*Stenopsocus*	*Caecilius*	*Cerobasis*	*Troctes*	*Liposcelis*	*Gliricola*	*Myrsidea*	*Pseudomenopon*	*Piagetiella*	*Trochiloecetes*	*Trimenopon*	*Bovicola*	*Ornithobius*	*Columbicola*	*Haematopinus*	*Hybophthirus*	*Pediculus*	*Phthirus*	*Haematomyzus*
74	?	?	0	?	0	0	?	0	0	?	0	0	0	0	?	?	0	0	0	?	0	?	0	?	0	?	0	0	?	0	0	0	0	?	0
75	?	?	0	?	0	0	?	0	0	?	0	0	0	0	?	?	0	0	0	?	0	?	0	?	0	?	0	0	?	0	0	0	0	?	0
76	?	?	0	?	0	0	?	0	0	?	1	1	1	1	?	?	1	1	1	?	0	?	1	?	1	?	1	1	?	1	1	1	1	?	1
77	?	?	0	?	0	0	?	0	0	?	0	0	0	0	?	?	0	0	0	?	0	?	0	?	0	?	0	0	?	0	0	0	0	?	0
78	?	?	0	?	1	0	?	0	0	?	0	0	0	0	?	?	1	0	0	?	0	?	0	?	0	?	0	0	?	0	0	0	0	?	1
79	?	?	0	?	0	0	?	0	0	?	1	0	0	0	?	?	0	0	1	?	0	?	0	?	0	?	0	0	?	0	0	0	0	?	0
80	?	?	0	?	1	1	?	1	1	?	0	0	0	0	?	?	0	0	0	?	0	?	0	?	0	?	0	0	?	0	0	0	0	?	0
81	?	?	0	?	?	0	?	0	0	0	0	0	0	0	?	?	0	0	0	?	0	?	0	?	0	?	0	0	?	0	0	0	0	?	0
82	?	?	0	?	1	1	?	1	0	?	0	0	0	0	?	?	0	0	0	?	0	?	0	?	0	?	0	0	?	0	0	0	0	?	0
83	?	?	0	?	0	0	?	0	0	?	0	0	0	0	?	?	0	0	0	?	0	?	0	?	0	?	0	0	?	0	0	0	0	?	0
84	?	?	-	?	-	-	?	-	-	?	3	0	0	0	?	?	4	4	4	?	-	?	4	?	4	?	4	0	?	0	0	0	0	?	0
85	?	?	0	?	0	0	?	0	0	?	0	0	0	0	?	?	0	0	0	?	0	?	0	?	0	?	0	0	?	0	0	0	0	?	1
86	?	?	0	?	1	1	?	1	1	?	0	0	0	0	?	?	1	1	1	?	1	?	1	?	1	?	1	1	?	1	1	1	0	?	1
87	?	?	0	?	0	0	?	0	0	?	0	0	0	0	?	?	0	0	0	?	0	?	0	?	0	?	0	0	?	0	0	0	0	?	0
88	?	?	0	?	0	0	?	0	0	?	1	1	1	1	?	?	1	1	0	?	0	?	0	?	0	?	0	0	?	0	0	0	0	?	0
89	?	?	0	?	0	0	?	0	0	?	0	0	0	0	?	?	1	1	1	?	1	?	1	?	1	?	0	0	?	0	0	0	0	?	1
90	?	?	0	?	0	0	?	0	0	?	0	0	0	0	?	?	0	0	0	?	0	?	0	?	0	?	0	0	?	0	0	0	0	?	1
91	?	?	0	?	0	0	?	0	0	?	0	0	0	0	?	?	0	0	0	?	0	?	0	?	0	?	0	0	?	0	0	0	0	?	1
92	?	?	0	?	0	0	?	0	0	?	0	0	0	0	?	?	0	0	0	?	0	?	0	?	0	?	0	0	?	0	0	0	0	?	1
93	?	?	0	?	0	0	?	0	0	?	0	0	0	0	?	?	0	0	0	?	0	?	0	?	0	?	0	0	?	0	0	0	0	?	1
94	?	?	0	?	0	0	?	0	0	?	0	0	0	0	?	?	0	0	1	?	0	?	0	?	0	?	0	0	?	0	0	0	0	?	0
95	?	?	0	?	0	0	?	0	0	?	0	0	0	0	?	?	0	0	0	?	0	?	0	?	0	?	0	0	?	0	0	0	0	?	0
96	?	?	1	?	1	1	?	1	1	?	1	1	1	1	?	?	1	1	1	?	1	?	1	?	1	?	1	0	?	0	0	0	1	?	0
97	?	?	0	?	?	0	?	0	0	?	0	0	0	0	?	?	0	0	0	?	0	?	0	?	0	?	0	0	?	0	0	0	0	?	0
98	?	?	0	?	?	0	?	0	0	?	0	0	0	0	?	?	0	0	0	?	0	?	0	?	0	?	0	0	?	0	0	0	0	?	0
99	?	?	0	?	?	0	?	0	0	?	0	0	0	0	?	?	0	0	0	?	0	?	0	?	0	?	0	0	?	0	0	0	0	?	1
100	?	?	0	?	?	0	?	0	0	?	0	0	0	0	?	?	0	0	0	?	0	?	0	?	0	?	0	0	?	0	0	0	0	?	0
101	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
102	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
103	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
104	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0

	Tibicina	*Idiocerus*	*Philaenus*	*Lepyronia*	*Platypleura*	*Oxyrhachis*	*Scolops*	*Melicharia**	*Dictyophara*	*Aeolothrips f.*	*Aeolothrips i.*	*Thrips*	*Haplothrips*	*Phlaeothrips*	*Psocus*	*Psococerastis*	*Stenopsocus*	*Caecilius*	*Cerobasis*	*Troctes*	*Liposcelis*	*Gliricola*	*Myrsidea*	*Pseudomenopon*	*Piagetiella*	*Trochiloecetes*	*Trimenopon*	*Bovicola*	*Ornithobius*	*Columbicola*	*Haematopinus*	*Hybophthirus*	*Pediculus*	*Phthirus*	*Haematomyzus*
105	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	0	0
106	0	0	0	0	0	0	-	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	-	-	-
107	1	0	1	0	1	0	-	1	1	1	1	-	-	-	1	1	1	1	1	1	1	1	1	0	0	1	0	0	-	-	-	-	-	-
108	1	1	1	0	1	1	0	1	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	0	1
109	0	?	0	-	1	?	-	0	0	0	0	-	-	-	1	1	1	0	0	1	1	1	0	1	1	0	1	1	1	1	-	0	-	-	0
110	0	0	0	-	0	0	-	0	0	0	0	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	-	-	0
111	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
112	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
113	1	1	1	1	1	1	1	1	1	1	1	-	-	-	1	1	1	1	1	1	1	0	1	0	0	0	0	1	0	-	-	-	-	-	-
114	0	0	0	-	0	-	-	0	0	0	0	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	-	-	-
115	0	0	0	0	0	0	0	0	0	1	1	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-	-	-
116	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-	-	-
117	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
118	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	1	1	1	0	0	0	0
119	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0
120	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0
121	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
122	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0
123	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
124	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
125	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
126	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	2	0	0	0	0	0	0	0
127	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
128	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	-	0	0	0	0	0	0	0
129	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
130	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0
131	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	?	-	-	-	-	?	-	-	-	-	-	-	-	-	-	-	-	-	-	-
132	-	-	-	-	-	-	-	-	-	0	0	0	0	0	?	?	0	?	0	0	?	0	0	0	0	0	0	-	0	0	0	0	0	0	0
133	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	?	-	?	-	-	?	-	-	-	-	-	-	-	-	-	-	-	-	-	-
134	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
135	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	Tibicina	*Idiocerus*	*Philaenus*	*Lepyronia*	*Platypleura*	*Oxyrhachis*	*Scolops*	*Melicharia**	*Dictyophara*	*Aeolothrips f.*	*Aeolothrips i.*	*Thrips*	*Haplothrips*	*Phlaeothrips*	*Psocus*	*Psococerastis*	*Stenopsocus*	*Caecilius*	*Cerobasis*	*Troctes*	*Liposcelis*	*Gliricola*	*Myrsidea*	*Pseudomenopon*	*Piagetiella*	*Trochiloecetes*	*Trimenopon*	*Bovicola*	*Ornithobius*	*Columbicola*	*Haematopinus*	*Hybophthirus*	*Pediculus*	*Phthirus*	*Haematomyzus*
136	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
137	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0
138	-	-	-	-	-	-	-	-	-	-	0	0	-	-	-	-	-	-	-	-	?	-	-	-	-	-	-	-	-	-	-	-	-	-
139	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	0	0	?	0	0	?	0	0	0	0	0	0	-	0	0	0	0	0	0	0
140	0	0	0	0	0	0	0	0	0	1	1	1	1	1	?	?	0	0	0	1	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0
141	-	-	-	-	-	-	-	-	-	0	0	1	2	2	?	?	-	-	-	2	?	-	-	-	-	-	-	-	-	-	-	-	-	-	-
142	0	0	0	0	0	0	0	0	0	1	1	0	1	1	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
143	0	0	0	0	0	0	-	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	-	0	0	0	0	0	0	0
144	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
145	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	1	?	0	0	0	-	0	0	0	0	0	0	0
146	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	1	1	1	0	0	-	0	0	0	0	0	0	0
147	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1
148	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	0	1	2
149	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1
150	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
151	?	1	1	?	1	1	1	1	1	1	1	1	1	1	?	?	1	1	1	?	1	1	1	1	1	1	1	1	1	1	?	1	1	?	1
152	?	1	1	?	1	1	1	1	1	1	1	1	1	1	?	?	1	1	1	?	1	1	1	1	1	1	1	1	1	1	?	1	1	?	1
153	?	0	0	?	0	0	0	0	0	0	0	0	0	0	?	?	1	1	1	?	1	1	1	1	0	1	1	0	0	0	?	0	1	?	0
154	?	0	0	?	0	0	1	0	0	0	0	0	0	0	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	?	0	0	?	0
155	2	2	2	2	2	2	3	2	0	0	0	0	0	0	?	?	4	4	4	?	0	0	0	0	0	0	0	0	0	5	1	0	1	1	1
156	?	1	1	?	1	1	?	1	1	1	1	1	1	1	?	?	1	1	1	?	1	1	1	1	1	1	1	1	1	1	?	1	1	?	1
157	?	1	1	?	1	1	?	1	1	1	1	1	1	1	?	?	1	1	1	?	1	1	1	1	1	1	1	1	1	1	?	1	1	?	1
158	?	1	0	?	1	1	?	1	0	0	0	0	0	0	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	?	0	0	?	0
159	?	1	0	?	1	1	?	1	0	0	0	0	0	0	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	?	0	0	?	0
160	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0
161	-	-	-	-	-	-	-	-	-	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	-	-	-	-	0
162	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	1	1	1	1	1	1	1	1
163	-	-	-	-	-	-	-	-	-	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	?	1	1	1	1	0	1	0	0	1
164	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	-	0	-	-	0
165	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
166	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1

	Tibicina	*Idiocerus*	*Philaenus*	*Lepyronia*	*Platypleura*	*Oxyrhachis*	*Scolops*	*Melicharia**	*Dictyophara*	*Aeolothrips f.*	*Aeolothrips i.*	*Thrips*	*Haplothrips*	*Phlaeothrips*	*Psocus*	*Psococerastis*	*Stenopsocus*	*Caecilius*	*Cerobasis*	*Troctes*	*Liposcelis*	*Gliricola*	*Myrsidea*	*Pseudomenopon*	*Piagetiella*	*Trochiloecetes*	*Trimenopon*	*Bovicola*	*Ornithobius*	*Columbicola*	*Haematopinus*	*Hybophthirus*	*Pediculus*	*Phthirus*	*Haematomyzus*
167	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
168	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	3	3	3	3	0
169	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	1	1	-
170	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
171	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	3	3	3	3	0
172	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	0	0
173	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
174	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
175	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
176	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
177	-	-	-	-	-	-	-	-	-	1	1	0	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
178	1	1	1	1	1	1	1	1	1	0	0	0	0	0	?	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
179	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0
180	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	?	0
181	1	1	1	1	1	1	2	2	2	2	?	?	?	3	?	?	2	?	?	?	?	?	?	2	?	?	?	?	?	?	?	?	?	?	?
182	?	1	?	?	?	?	?	?	?	?	?	0	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
183	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	1	0	1	1	0	1	0	1	1	1	1	0	0	0	0	1
184	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	0	0	-	0	-	0	4	?	0	-	-	-	-	?
185	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	0	0	-	0	-	0	4	?	0	-	-	-	-	?
186	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
187	0	0	0	0	0	0	0	0	0	3	3	3	3	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
188	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
189	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
190	4	0	4	4	0	0	5	0	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
191	0	0	0	?	?	?	?	?	0	1	1	1	1	1	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
192	-	-	-	?	?	?	?	?	-	1	1	1	1	1	?	?	-	-	-	?	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
193	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
194	0	0	0	0	0	0	0	0	0	1	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
195	?	?	?	?	?	?	?	?	?	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
196	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
197	?	?	?	?	?	?	?	?	?	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

	Tibicina	*Idiocerus*	*Philaenus*	*Lepyronia*	*Platypleura*	*Oxyrhachis*	*Scolops*	*Melicharia**	*Dictyophara*	*Aeolothrips f.*	*Aeolothrips i.*	*Thrips*	*Haplothrips*	*Phlaeothrips*	*Psocus*	*Psococerastis*	*Stenopsocus*	*Caecilius*	*Cerobasis*	*Troctes*	*Liposcelis*	*Gliricola*	*Myrsidea*	*Pseudomenopon*	*Piagetiella*	*Trochiloecetes*	*Trimenopon*	*Bovicola*	*Ornithobius*	*Columbicola*	*Haematopinus*	*Hybophthirus*	*Pediculus*	*Phthirus*	*Haematomyzus*
198	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	1	1	1	1	0	1	0	1	1	0	1	1	0
199	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	?	0	1	0	1	1	1	-	1	-	0	1	-	1	1	0
200	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
201	0	1	1	0	1	1	0	1	0	1	1	1	1	1	0	1	1	1	1	0	1	0	1	1	0	0	0	1	1	0	0	0	0	0	0
202	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
203	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
204	0	1	1	0	1	1	0	1	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
205	-	1	1	-	1	1	-	1	-	-	-	-	-	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
206	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
207	0	1	0	0	1	1	0	1	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
208	1	1	1	1	1	1	1	1	1	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
209	0	1	0	0	1	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
210	-	0	-	-	0	-	-	-	-	-	-	-	-	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
211	0	0	0	0	1	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
212	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
213	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	1	1	0	1	0	0	?
214	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	1	1	-	1	-	-	?
215	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	1	1	-	1	-	-	?
216	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	2	2	2	2	2	?	2	2	2	-	2	-	-	?
217	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	2	2	2	?	?	?	0	?	?	0	?	0	-	0	-	-	?
218	?	0	?	?	?	?	?	?	?	?	?	0	?	?	0	0	0	0	0	0	0	0	0	0	0	?	?	0	?	0	-	0	-	-	?
219	?	0	?	?	?	?	?	?	?	?	?	0	?	?	0	0	0	0	0	0	0	0	0	0	0	?	?	0	?	0	-	0	-	-	?
220	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	1	1	-	1	-	-	?
221	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	-	0	-	-	?
222	0	0	0	0	0	0	0	0	0	1	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	?	-	-	-	-	-	-	-	?
223	0	0	0	0	0	0	0	0	0	1	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	?	-	-	-	-	-	-	-	?
224	2	2	0	?	2	2	?	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	-	-	-	-	-	-	-	?
225	1	1	1	?	1	1	?	1	1	1	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	?	-	-	-	-	-	-	-	?
226	?	2	2	?	2	2	?	2	1	2	2	2	2	2	-	-	-	-	-	-	-	-	-	-	-	-	?	-	-	-	-	-	-	-	?
227	1	1	1	1	1	1	1	1	1	0	0	0	0	0	?	?	1	1	1	?	1	?	1	1	1	?	?	1	?	0	-	0	-	-	?
228	1	1	0	1	1	1	1	1	1	-	-	-	-	-	?	?	0	0	0	?	0	?	0	0	0	?	?	?	?	-	-	-	-	-	?

	Tibicina	*Idiocerus*	*Philaenus*	*Lepyronia*	*Platypleura*	*Oxyrhachis*	*Scolops*	*Melicharia**	*Dictyophara*	*Aeolothrips f.*	*Aeolothrips i.*	*Thrips*	*Haplothrips*	*Phlaeothrips*	*Psocus*	*Psococerastis*	*Stenopsocus*	*Caecilius*	*Cerobasis*	*Troctes*	*Liposcelis*	*Gliricola*	*Myrsidea*	*Pseudomenopon*	*Piagetiella*	*Trochiloecetes*	*Trimenopon*	*Bovicola*	*Ornithobius*	*Columbicola*	*Haematopinus*	*Hybophthirus*	*Pediculus*	*Phthirus*	*Haematomyzus*
229	2	2	?	2	2	2	2	2	2	-	-	-	-	-	?	?	0	?	?	?	?	?	?	?	?	?	?	?	-	-	-	-	-	?
230	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	?
231	-	-	-	-	-	-	-	-	-	0	0	-	-	-	0	-	-	-	-	-	-	0	-	-	-	-	0	-	-	-	-	-	-	?
232	-	-	-	-	-	-	-	-	-	0	0	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	?
233	-	-	-	-	-	-	-	-	-	1	1	-	-	-	0	-	-	-	-	-	-	0	-	-	-	-	0	-	-	-	-	-	-	?
234	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	?
235	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	-	-	-	-	-	-	0
236	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-	-	-	0
237	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	-	-	-	-	-	-	0
238	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-	-	-	0
239	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		-	-	-	-	-	0
240	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-	-	-	0
241	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-	-	-	0
242	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	?
243	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	?
244	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	?
245	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	?
246	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	?
247	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	1	1	1	1	1	1	-	1	0	0	0	0	0	0	?
248	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	1	0	?
249	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	1	1	1	?
250	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	1	0	0
251	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	1	0	1	0
252	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	1	1	0	?
253	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
254	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0
255	-	-	-	-	-	-	-	-	-	1	1	1	0	0	2	2	2	2	2	2	2	0	2	2	2	2	2	-	-	-	-	-	-	-	-
256	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
257	1	0	1	1	1	1	1	1	1	1	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
258	1	1	1	1	1	1	0	0	0	1	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
259	2	1	2	2	2	1	-	-	-	2	2	2	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

	Tibicina	*Idiocerus*	*Philaenus*	*Lepyronia*	*Platypleura*	*Oxyrhachis*	*Scolops*	*Melicharia**	*Dictyophara*	*Aeolothrips f.*	*Aeolothrips i.*	*Thrips*	*Haplothrips*	*Phlaeothrips*	*Psocus*	*Psococerastis*	*Stenopsocus*	*Caecilius*	*Cerobasis*	*Troctes*	*Liposcelis*	*Gliricola*	*Myrsidea*	*Pseudomenopon*	*Piagetiella*	*Trochiloecetes*	*Trimenopon*	*Bovicola*	*Ornithobius*	*Columbicola*	*Haematopinus*	*Hybophthirus*	*Pediculus*	*Phthirus*	*Haematomyzus*
260	0	1	1	?	?	?	?	?	0	0	0	0	0	0	?	?	0	?	?	0	0	1	1	1	0	1	0	1	1	1	1	1	1	1
261	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
262	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	1	1	1	1	1	0
263	0	0	0	0	0	0	0	0	0	3	3	3	3	3	?	0	0	0	0	2	2	1	3	2	2	2	?	2	2	2	2	2	2	-
264	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
265	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
266	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	1	0	1	1	1	1	1	0	1	1	1	1	0	0
267	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	-	0	-	0	0	0	0	0	-	1	1	1	0	-	-
268	1	1	1	1	1	1	1	1	1	?	?	?	?	?	1	1	1	1	1	1	1	1	1	1	1	1	?	1	1	1	0	1	0	0
269	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
270	0	0	0	0	0	0	0	0	0	1	1	1	1	1	?	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0
271	-	-	-	-	-	-	-	-	-	0	0	1	1	1	?	0	0	0	0	0	0	2	2	2	2	0	2	-	-	-	-	-	-	-
272	0	0	0	0	0	0	0	0	0	1	1	0	0	0	?	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
273	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	1	1	1	1	?	1	0	0	0	0	0	1	0	0	0	0	0	0	0
274	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	1	1	1	?	1	1	0	0	0	0	0	0	0	0	0	0	0	0
275	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	1	1	1	?	1	0	1	1	1	1	1	0	0	0	0	0	0	0
276	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	1	1	1	?	1	0	1	1	1	0	1	0	0	0	0	0	0	0
277	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0
278	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
279	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	?	0	0	0	1	1	1	1	0	0	0	0	0	0	0
280	1	0	1	1	1	0	0	0	0	1	1	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
281	0	-	0	0	0	-	-	-	-	1	1	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	-
282	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
283	1	1	0	1	1	1	0	0	0	1	1	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	0	0
284	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
285	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0
286	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	?	0	1	0	0	0	0	0	0	0	0	0	0	0	0
287	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
288	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0
289	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
290	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	Tibicina	*Idiocerus*	*Philaenus*	*Lepyronia*	*Platypleura*	*Oxyrhachis*	*Scolops*	*Melicharia**	*Dictyophara*	*Aeolothrips f.*	*Aeolothrips i.*	*Thrips*	*Haplothrips*	*Phlaeothrips*	*Psocus*	*Psococerastis*	*Stenopsocus*	*Caecilius*	*Cerobasis*	*Troctes*	*Liposcelis*	*Gliricola*	*Myrsidea*	*Pseudomenopon*	*Piagetiella*	*Trochiloecetes*	*Trimenopon*	*Bovicola*	*Ornithobius*	*Columbicola*	*Haematopinus*	*Hybophthirus*	*Pediculus*	*Phthirus*	*Haematomyzus*
291	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
292	2	2	2	1	2	2	2	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
293	0	0	0	0	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
294	0	0	0	0	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
295	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
296	0	0	0	0	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
297	0	0	0	0	0	0	0	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
298	0	0	0	0	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
299	1	1	1	1	1	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
300	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
301	?	?	?	?	?	?	?	?	?	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	1	1	1	0	0	0	0	0
302	?	?	?	?	?	?	?	?	?	1	1	1	1	1	0	?	1	1	1	1	1	1	0	1	0	?	0	1	1	1	-	-	-	-	-
303	?	?	?	?	?	?	?	?	?	1	1	1	1	1	1	?	1	1	1	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-	-
304	?	?	?	?	?	?	?	?	?	1	?	1	1	1	0	?	0	0	0	?	0	0	1	0	0	0	0	0	0	0	-	-	-	-	-
305	?	?	?	?	?	?	?	?	?	1	1	1	1	1	1	1	1	1	1	1	1	?	1	1	1	?	1	0	1	0	0	0	0	0	0
306	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	?	0	-	0	-	-	-	-	-	-
307	?	?	?	?	?	?	?	?	?	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	-	0	-	-	-	-	-	-
308	-	-	-	-	-	-	-	-	-	1	1	1	1	1	0	0	0	0	0	0	0	?	0	0	0	0	0	-	0	-	-	-	-	-	-
309	?	?	?	?	?	?	?	?	?	0	0	0	0	0	1	?	1	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
310	?	?	?	?	?	?	?	?	?	-	-	-	-	-	0	?	0	?	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
311	?	?	?	?	?	?	?	?	?	-	-	-	-	-	1	?	1	?	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
312	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	?	1	?	1	1	1	1	1	1	0	0	0	0	0
313	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0
314	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0
315	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	1	1	-
316	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0
317	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0	0	0	0	1
318	-	-	-	-	-	-	-	-	-	0	0	1	1	1	2	2	2	2	2	2	2	2	2	2	-	2	2	2	2	-	-	-	-	2
319	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	-	-	-	-	1
320	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
321	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0

	Tibicina	*Idiocerus*	*Philaenus*	*Lepyronia*	*Platypleura*	*Oxyrhachis*	*Scolops*	*Melicharia**	*Dictyophara*	*Aeolothrips f.*	*Aeolothrips i.*	*Thrips*	*Haplothrips*	*Phlaeothrips*	*Psocus*	*Psococerastis*	*Stenopsocus*	*Caecilius*	*Cerobasis*	*Troctes*	*Liposcelis*	*Gliricola*	*Myrsidea*	*Pseudomenopon*	*Piagetiella*	*Trochiloecetes*	*Trimenopon*	*Bovicola*	*Ornithobius*	*Columbicola*	*Haematopinus*	*Hybophthirus*	*Pediculus*	*Phthirus*	*Haematomyzus*
322	0	0	?	0	0	0	0	0	1	1	1	1	1	1	1	?	1	1	1	1	1	?	1	1	1	1	1	1	1	0	0	0	0	1
323	-	-	?	-	-	-	-	-	2	0	0	0	0	0	0	?	0	0	0	0	0	?	?	?	0	?	0	?	?	0	-	-	-	-	0
324	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
325	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
326	3	3	3	3	3	3	3	3	3	1	1	1	1	1	0	0	0	0	?	?	?	?	?	1	?	1	?	1	1	1	5	5	5	5	0
327	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	0
328	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	-	-	1	0	1	1	-
329	?	?	?	?	?	?	?	?	?	0	0	0	0	0	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
330	?	?	?	?	?	?	?	?	?	1	1	1	0	0	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
331	?	?	?	?	?	?	?	?	?	1	1	1	1	1	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
332	0	?	0	0	0	0	0	0	?	0	0	0	0	0	?	?	1	1	1	?	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0
333	?	?	?	?	?	?	?	?	?	0	0	0	0	0	?	?	1	1	1	?	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
334	?	?	?	?	?	?	?	?	?	-	-	-	-	-	?	?	0	0	0	?	1	1	1	1	1	1	1	1	1	1	2	1	1	1	-
335	?	?	?	?	?	?	?	?	?	-	-	-	-	-	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	2	1	2	2	-
336	?	?	?	?	?	?	?	?	?	1	1	0	0	0	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
337	?	?	?	?	?	?	?	?	?	1	1	1	1	1	?	?	1	1	1	?	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0
338	0	0	0	0	0	0	0	0	0	1	0	0	0	0	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
339	0	0	0	0	0	0	0	0	0	1	0	1	1	1	?	?	1	1	1	?	1	1	1	1	0	0	1	1	1	1	1	1	1	1	0
340	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	1	1	1	?	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
341	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
342	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	0
343	1	1	1	1	1	1	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
344	0	0	0	0	0	0	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	-
345	1	1	1	1	1	1	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
346	1	1	1	1	1	1	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
347	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
348	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
349	1	1	1	1	1	1	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
350	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
351	1	1	1	1	1	1	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
352	0	1	1	1	1	1	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0

	Tibicina	*Idiocerus*	*Philaenus*	*Lepyronia*	*Platypleura*	*Oxyrhachis*	*Scolops*	*Melicharia**	*Dictyophara*	*Aeolothrips f.*	*Aeolothrips i.*	*Thrips*	*Haplothrips*	*Phlaeothrips*	*Psocus*	*Psococerastis*	*Stenopsocus*	*Caecilius*	*Cerobasis*	*Troctes*	*Liposcelis*	*Gliricola*	*Myrsidea*	*Pseudomenopon*	*Piagetiella*	*Trochiloecetes*	*Trimenopon*	*Bovicola*	*Ornithobius*	*Columbicola*	*Haematopinus*	*Hybophthirus*	*Pediculus*	*Phthirus*	*Haematomyzus*
353	0	0	0	0	1	0	0	0	0	0	0	0	0	0	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0
354	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0
355	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0
356	0	1	0	0	0	0	0	0	1	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	0
357	-	2	-	-	-	-	-	-	0	-	-	-	-	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	-	?	?	?	?	-
358	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
359	0	0	0	0	0	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
360	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0
361	0	0	0	0	0	1	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
362	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0
363	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0
364	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0
365	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0
366	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
367	0	0	0	0	0	0	0	0	0	1	1	1	1	1	?	?	1	1	1	?	1	?	1	1	1	1	0	1	1	1	1	1	1	0
368	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	2	2	2	3
369	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	1	1	1	1	1
370	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	?	0	0	0	0	0	?	1	1	1	1	0	1	0	1	1	1	1	0
371	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0
372	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0
373	0	0	0	0	0	0	0	0	0	1	1	1	1	1	?	?	1	1	1	?	1	0	1	1	1	1	1	1	1	1	1	1	1	0
374	-	-	-	-	-	-	-	-	-	0	0	0	1	1	?	?	0	0	0	?	0	-	0	0	0	0	0	0	0	0	0	0	0	0	-
375	0	0	0	0	0	0	0	0	0	1	1	1	1	1	?	?	1	1	1	?	0	0	0	1	1	1	0	1	1	1	1	1	1	0
376	-	-	-	-	-	-	-	-	-	1	?	1	1	1	?	?	0	0	0	?	-	?	-	0	0	0	-	0	0	0	0	0	0	0	-
377	-	-	-	-	-	-	-	-	-	1	1	1	1	1	?	?	0	0	0	?	-	?	-	0	0	0	-	0	0	0	0	0	0	0	-
378	0	1	1	0	0	0	0	1	1	1	1	1	1	1	?	?	1	1	1	?	1	?	1	1	1	1	1	1	1	1	1	1	1	1
379	-	2	2	-	-	-	-	2	2	0	?	0	1	1	?	?	2	2	2	?	2	?	2	2	2	2	2	2	2	2	2	2	2	2
380	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	?	0	?	0	0	0	0	0	0	1	0	1	0	0	0	0
381	0	0	0	0	0	0	0	0	0	0	1	0	1	1	?	?	0	0	0	?	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0
382	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
383	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	Tibicina	*Idiocerus*	*Philaenus*	*Lepyronia*	*Platypleura*	*Oxyrhachis*	*Scolops*	*Melicharia**	*Dictyophara*	*Aeolothrips f.*	*Aeolothrips i.*	*Thrips*	*Haplothrips*	*Phlaeothrips*	*Psocus*	*Psococerastis*	*Stenopsocus*	*Caecilius*	*Cerobasis*	*Troctes*	*Liposcelis*	*Gliricola*	*Myrsidea*	*Pseudomenopon*	*Piagetiella*	*Trochiloecetes*	*Trimenopon*	*Bovicola*	*Ornithobius*	*Columbicola*	*Haematopinus*	*Hybophthirus*	*Pediculus*	*Phthirus*	*Haematomyzus*
384	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
385	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	1	1	0	0	0	?	1	1	1	1	1	0
386	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	1	1	0	1	0	1	1	1	1	1	1	1
387	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
388	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
389	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	?	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
390	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
391	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	?	1	1	1	?	1	?	1	1	1	1	1	1	1	1	1	1	1	1
392	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
393	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	1	?	?	?	1	1	1	1	1	1	1	1	1	1	1	0	1
394	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
395	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	-
396	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	?	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-
397	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	?	0	1	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	-
398	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0
399	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	?	0	0	0	0	0	0	0	0	1	0	0	0	0	1	?	0	-	-
400	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	0	0	0	1	0	1	0	0	?	0	1	0	0	-	-
401	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	1	-	-	?	-	2	-	-	-	-
402	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	-	-
403	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
404	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	1	0	1	1	0	1	1	1	0	0
405	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	0	0	0	-	0	-	0	0	-	0	1	1	-	-	-
406	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	0	0	0	-	0	-	0	1	-	0	0	0	-	-	-
407	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	0	0
408	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	?	1	1	0	1	1	0	1	0	0	0	0	1	-	1	0	0	-	-	-
409	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	1
410	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0
411	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	**1**	**1**	**1**	0
412	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
413	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0
414	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	1	1	-

	Tibicina	*Idiocerus*	*Philaenus*	*Lepyronia*	*Platypleura*	*Oxyrhachis*	*Scolops*	*Melicharia**	*Dictyophara*	*Aeolothrips f.*	*Aeolothrips i.*	*Thrips*	*Haplothrips*	*Phlaeothrips*	*Psocus*	*Psococerastis*	*Stenopsocus*	*Caecilius*	*Cerobasis*	*Troctes*	*Liposcelis*	*Gliricola*	*Myrsidea*	*Pseudomenopon*	*Piagetiella*	*Trochiloecetes*	*Trimenopon*	*Bovicola*	*Ornithobius*	*Columbicola*	*Haematopinus*	*Hybophthirus*	*Pediculus*	*Phthirus*	*Haematomyzus*
415	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0
416	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	0	0	-
417	1	1	1	1	1	1	1	1	1	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	-	-	1
418	?	?	?	?	?	?	?	?	?	1	1	1	1	1	?	?	?	?	?	?	?	?	1	1	?	1	?	1	1	?	?	1	?	?	?
419	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
420	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	**0**	**1**	**1**	**1**	0	1	**1**	?	**1**	**0**	0	**0**	0	0
421	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0
422	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0
423	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	1	1	1	?	0	0	0	0	0	1	1	1	1	?	0	0	0	0	0
424	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	1	1	1	?	0	0	0	1	0	1	1	1	1	?	0	0	0	0	0
425	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	?	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
426	?	0	0	?	?	?	?	?	0	0	0	0	1	1	0	?	0	0	0	0	0	1	1	1	1	0	0	0	1	1	0	0	0	0	1
427	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	1	1	1	?	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0
428	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	?	0	0	0	?	0	-	1	1	0	0	0	0	0	0	0	0	0	0	-
429	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	1	?	1	0	0	1	0	0	0	0	0	0	1	1	0	0	0
430	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	?	-	-	1	?	0	-	-	0	-	-	-	-	-	-	1	0	-	-	-
431	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
432	0	0	0	0	0	0	0	0	0	1	1	1	1	1	?	?	1	1	1	?	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
433	-	-	-	-	-	-	-	-	-	0	0	0	1	1	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-
434	-	-	-	-	-	-	-	-	-	0	0	0	0	0	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	1	1	0	1	-
435	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	1	1	?	0	0	1	1	0	1	0	1	1	0	0	0	0	0	0
436	?	?	?	?	?	?	?	?	?	1	1	1	0	0	?	?	1	1	1	?	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0
437	?	?	?	?	?	?	?	?	?	1	1	1	1	1	?	?	1	1	1	?	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0
438	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
439	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
440	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?	1	1	1	?	?	1	1	1	1	1	1	1	1	1	1	?	1	0	0	1
441	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?	1	1	1	?	1	1	1	1	1	1	1	1	1	1	1	?	1	-	-	0
442	0	0	0	0	0	0	0	0	0	1	1	1	1	1	?	?	1	1	1	?	0	1	1	1	0	1	0	1	1	1	1	1	1	1	0
443	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	1	0	0	?	0	0	1	1	0	0	0	1	1	1	0	0	0	0	0
444	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	?	-	-	0	1	-	-	-	0	0	1	-	-	-	-	-
445	0	0	0	0	1	0	0	0	0	0	0	0	0	0	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	Tibicina	*Idiocerus*	*Philaenus*	*Lepyronia*	*Platypleura*	*Oxyrhachis*	*Scolops*	*Melicharia**	*Dictyophara*	*Aeolothrips f.*	*Aeolothrips i.*	*Thrips*	*Haplothrips*	*Phlaeothrips*	*Psocus*	*Psococerastis*	*Stenopsocus*	*Caecilius*	*Cerobasis*	*Troctes*	*Liposcelis*	*Gliricola*	*Myrsidea*	*Pseudomenopon*	*Piagetiella*	*Trochiloecetes*	*Trimenopon*	*Bovicola*	*Ornithobius*	*Columbicola*	*Haematopinus*	*Hybophthirus*	*Pediculus*	*Phthirus*	*Haematomyzus*
446	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	1
447	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0
448	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0
449	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0
450	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0
451	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0
452	?	?	1	?	?	?	?	?	1	1	1	1	1	1	?	?	1	1	1	?	1	?	1	1	?	1	1	1	1	1	1	1	1	1
453	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	1	0	?	0	?	0	0	1	1	1	0	0	1	1	1	1	0	0
454	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	1	1	1	?	1	?	1	0	1	1	1	1	0	1	1	1	0	0	1
455	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	0	0	0	?	0	?	0	-	0	1	0	1	-	0	1	1	-	-	0
456	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	1	1	1	?	1	?	0	-	0	1	0	1	-	1	0	1	-	-	0
457	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	?	0	0	0	1	0	0	0	0	1	1	1	0
458	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	1	1	1	1	0
459	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	-	-	-	-	-	?	-	-	-	-	-	-	-	-	1	1	0	0	-
460	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0
461	?	2	?	?	?	2	?	?	?	3	3	3	3	3	-	?	-	-	-	-	-	?	-	-	-	-	-	-	-	-	-	-	-	-	-
462	?	1	?	?	?	1	?	?	?	1	1	1	1	1	-	?	-	-	-	-	-	?	-	-	-	-	-	-	-	-	-	-	-	-	-
463	?	2	?	?	?	2	?	?	?	3	3	3	3	3	?	?	?	?	?	?	?	?	5	4	?	?	6	?	?	?	?	?	?	?	?
464	?	2	?	?	?	2	?	?	?	3	3	3	3	3	?	?	?	?	?	?	?	?	3	3	?	?	3	?	?	?	?	?	?	?	?
465	?	0	?	?	?	0	?	?	?	2	2	2	2	2	?	?	?	?	?	?	?	?	1	0	?	?	3	?	?	?	?	?	?	?	?
466	?	2	?	?	?	2	?	?	?	0	0	0	0	0	?	?	?	?	?	?	?	?	2	2	?	?	2	?	?	?	?	?	?	?	?
467	?	2	?	?	?	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	3	3	?	?	?	?	?	?	?	?	?	?	?
468	?	1	1	?	?	1	?	?	1	1	1	1	1	1	?	?	?	0	0	?	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0
469	?	2	2	?	?	2	?	?	2	0	0	0	0	0	?	?	?	-	-	?	-	?	-	-	-	-	-	-	-	-	-	-	-	-	-
470	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0
471	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	?	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0
472	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	1	1	?	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0
473	1	1	1	1	?	?	1	?	1	1	1	1	1	1	2	2	2	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
474	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0
475	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
476	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1

	Tibicina	*Idiocerus*	*Philaenus*	*Lepyronia*	*Platypleura*	*Oxyrhachis*	*Scolops*	*Melicharia**	*Dictyophara*	*Aeolothrips f.*	*Aeolothrips i.*	*Thrips*	*Haplothrips*	*Phlaeothrips*	*Psocus*	*Psococerastis*	*Stenopsocus*	*Caecilius*	*Cerobasis*	*Troctes*	*Liposcelis*	*Gliricola*	*Myrsidea*	*Pseudomenopon*	*Piagetiella*	*Trochiloecetes*	*Trimenopon*	*Bovicola*	*Ornithobius*	*Columbicola*	*Haematopinus*	*Hybophthirus*	*Pediculus*	*Phthirus*	*Haematomyzus*
477	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	1
478	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
479	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
480	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1
481	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
482	?	?	0	?	?	?	?	?	0	1	1	1	1	1	?	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0
483	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?	1	1	1	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0
484	?	?	0	?	?	?	?	?	0	0	0	0	0	0	?	?	1	1	1	?	0	?	0	1	0	1	0	1	1	0	0	0	0	0	1
485	1	1	1	0	1	1	1	1	1	1	1	1	0	0	?	?	1	1	1	?	1	?	1	1	0	1	1	1	1	1	1	1	1	1	1
486	1	1	1	1	1	1	1	1	1	1	0	0	0	0	?	?	1	1	1	1	1	?	1	1	1	1	1	1	1	1	1	1	1	1	1
487	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?	1	1	1	?	1	?	1	1	1	1	1	1	1	1	1	1	1	1	1
488	?	1	1	1	1	1	1	0	1	0	0	1	1	1	?	?	1	1	1	?	1	?	1	1	1	0	1	1	1	1	1	1	1	1	1
489	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	?	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0
490	1	1	1	0	1	1	0	1	1	1	0	0	0	0	?	?	1	1	1	?	1	?	1	1	1	0	1	0	0	0	0	0	0	0	0
491	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	?	0	?	1	1	0	0	0	0	1	0	0	0	0	0	0
492	1	1	1	0	0	0	0	0	0	1	1	1	1	1	?	?	1	1	1	?	1	?	1	1	1	0	0	1	1	1	1	1	1	1	0
493	1	1	1	1	1	1	1	1	1	0	0	0	0	0	?	?	1	1	1	?	1	?	1	1	1	1	1	1	1	1	1	1	0	0	1
494	1	0	1	0	1	1	0	1	1	0	0	0	0	0	?	?	0	0	0	?	0	?	1	1	0	1	1	1	0	1	1	1	1	1	1
495	1	1	1	0	1	1	0	0	0	0	0	0	0	0	?	?	0	0	0	?	0	?	1	1	0	1	1	1	1	0	1	1	1	1	0
496	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	?	0	?	0	0	0	0	0	1	1	1	0	1	0	0	0
497	?	?	1	?	?	?	?	?	1	0	0	0	0	0	?	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0
498	?	?	0	?	?	?	?	?	0	1	1	1	1	1	?	?	1	1	1	1	?	?	1	1	1	1	1	1	1	1	1	1	1	0	1
499	?	1	1	?	?	?	?	?	1	1	1	1	1	1	1	?	1	1	1	1	?	?	1	1	1	1	1	1	1	1	?	1	1	?	0	1
500	?	1	1	?	?	?	?	?	1	1	1	1	2	2	0	?	1	1	1	1	?	?	1	1	0	1	1	1	1	?	1	1	?	-	1
501	?	1	1	?	?	?	?	?	1	1	1	1	1	1	?	?	1	1	1	1	?	?	1	1	?	1	1	1	1	?	1	1	?	-	1
502	?	4	4	?	?	?	?	?	4	4	4	4	4	4	?	?	?	5	4	?	?	?	5	0	?	?	4	5	?	?	5	?	?	-	5
503	?	1	1	?	?	?	?	?	1	1	1	1	1	1	?	?	1	1	1	1	?	?	1	1	?	1	1	1	1	?	1	1	?	-	?
504	?	1	0	?	?	?	?	?	0	1	1	1	1	1	?	?	1	1	0	1	?	?	?	?	?	1	1	0	?	?	1	?	?	-	?
505	?	1	1	?	?	?	?	?	1	1	?	1	1	1	?	?	0	0	?	?	?	?	0	0	?	0	0	0	?	?	0	0	?	-	0
506	?	1	1	?	?	?	?	?	1	1	1	1	1	1	?	?	1	1	0	1	?	?	?	1	?	1	1	0	?	?	0	?	?	-	1
507	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	Tibicina	*Idiocerus*	*Philaenus*	*Lepyronia*	*Platypleura*	*Oxyrhachis*	*Scolops*	*Melicharia**	*Dictyophara*	*Aeolothrips f.*	*Aeolothrips i.*	*Thrips*	*Haplothrips*	*Phlaeothrips*	*Psocus*	*Psococerastis*	*Stenopsocus*	*Caecilius*	*Cerobasis*	*Troctes*	*Liposcelis*	*Gliricola*	*Myrsidea*	*Pseudomenopon*	*Piagetiella*	*Trochiloecetes*	*Trimenopon*	*Bovicola*	*Ornithobius*	*Columbicola*	*Haematopinus*	*Hybophthirus*	*Pediculus*	*Phthirus*	*Haematomyzus*
508	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
509	?	0	0	?	?	?	?	?	0	0	0	0	0	0	0	?	0	0	0	0	?	?	0	0	?	0	0	0	0	?	0	1	0	0	0
510	0	0	0	0	0	0	0	0	0	1	0	0	1	1	?	?	0	0	?	?	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0
511	0	0	0	0	0	0	0	0	0	1	0	0	0	0	?	?	0	0	0	?	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0
512	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	?	0	?	0	0	0	0	0	0	0	0	0	0	0	0	1
513	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	?	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0
514	1	1	1	1	?	?	1	?	1	1	1	1	1	1	?	?	1	1	1	1	1	?	1	1	1	1	1	1	1	1	1	1	1	1	1
515	0	?	0	0	?	?	0	?	0	0	0	0	0	0	?	?	0	0	0	1	1	?	1	1	1	1	1	1	1	1	1	1	1	1	1
516	0	0	0	?	?	?	0	?	1	0	0	0	0	0	?	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0
517	0	0	0	0	?	?	0	?	0	1	1	1	1	1	?	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0
518	0	0	0	0	?	?	0	?	0	0	0	1	0	0	?	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0
519	0	?	1	?	0	1	?	0	1	0	0	0	0	0	?	?	0	1	0	1	0	?	0	0	1	0	0	0	0	0	0	0	0	0	0
520	1	?	1	1	1	1	1	1	1	0	0	0	0	0	?	?	0	1	1	1	1	?	0	1	1	1	1	0	0	0	0	1	1	1	1
521	?	?	0	?	?	?	?	?	0	1	1	1	1	1	?	?	1	1	1	?	1	?	1	?	0	?	?	?	?	1	?	?	1	?	1
522	0	0	0	0	?	?	0	?	0	0	0	0	0	0	?	?	0	0	0	0	0	?	0	0	0	0	0	1	0	1	1	1	1	1	0
523	-	-	-	-	?	?	-	?	-	-	-	-	-	-	?	?	-	-	-	-	-	?	-	-	-	-	-	0	-	0	1	1	1	?	-

3.5 Results of cladistic analyses

The initial cladistic analysis of 397 phylogenetically relevant characters including the complete sampling of 72 taxa (see also Tabs. 2, 3) resulted into two different phylogenies calculated either with NONA or with TNT. NONA yielded different numbers (6, 9, 11, 12, 14, 17, 24) of most parsimonious trees in subsequent runs. The strict consensus (1381 steps, Ci: 34, Ri: 75) is presented in Fig. A1. The result obtained with TNT is a group of ten most parsimonious trees (1375 steps) with the strict consensus shown in Fig. A2 (applying the "Move branch mode" implemented in WinClada yielded 1391 steps in the TNT-consensus tree, Ci: 33, Ri: 75). Both cladograms differ in the position of Troctomorpha. In NONA Troctomorpha together with (Trogiomorpha + Psocomorpha) form a monophylum Psocoptera, which is the sister group to all other Acercaria, implying paraphyletic Psocodea (apomorpies see below). The alternative cladogram calculated with TNT shows Psocoptera as paraphyletic with non-monophyletic Troctomorpha (see also Fig. 3) as sister group to Phthiraptera. The clade Psocodea is placed as the sister group to Condylognatha. Psocodea is supported by the presence of an antennal rupture-facilitating device (Seeger 1975) (143/1), the tri-furctated tip of the lacinia (217/2), the fusion of the cardo with the stipes (232/1), the swollen paired ovoid sclerites (404/1), the paired filamentous ligaments connecting the sitophore and the ovoid slerite (407/1), the presence of a water vapor uptaking facility (420/1), and the presence of the epipharyngeal sclerite (454/1).

Other differences between the results of cladistic analyses with the two programs are the following: the unresolved position of *Thrips* in TNT; the position of *Bovicola* within Ischnocera either as sister group to *Ornithobius* (TNT) or *Columbicola* (NONA); and either the monophyly (NONA) or paraphyly (TNT) of Menoponidae (Amblycera).

Common to both strict consensus cladograms (NONA and TNT) are the positions of *Melicharia* (Fulgoromorpha), *Aleurolobus* (Aleyrodoidea), and *Macrosiphum* (Aphidoidea). They are highly questionable and contradict the monophyly of the traditional groups Fulgoromorpha, Aleyrodoidea, and Aphidoidea, respectively (e.g. Heie 1987; Campbell et al. 1994, 1995; von Dohlen & Moran 1995; Yoshizawa & Saigusa 2001; Urban & Cryan 2007). Thus, their non-monophyly in the present study is considered as an artifact. As the main focus of this contribution is the higher-level phylogeny of Acercaria, and as the monophyly of Fulgoromorpha and Aleyrodoidea is sufficiently documented, it appeared justifiable to exclude *Melicharia* and *Aleurolobus* from a second set of the cladistic analysis.

The cladistic analysis with the revised taxon sampling (70 taxa) yielded 41 most parsimonious trees with NONA (1352 steps, Ci: 34, Ri: 75) and ten with TNT (1342 steps). The strict consenus trees obtained with both programs are identical and discussed in detail below

(Fig. 29). Apomorphies of outgroup and ingroup taxa (character optimization: unambiguous) are listed in the following. Homoplasious characters are set in *italics*.

((*Macroxyela* + *Zorotypus*) + (*Osmylus* + (*Schizodactylus* + Acercaria))) (apomorphy-complex 1) (Bremer Support = BS: 3)

0mx4, M. tentoriostipitalis anterior absent (265/0); “Labralleiste” absent (370/0); lingua absent (423/0); superlingua absent (424/0); 0hy3, M. craniohypopharyngealis absent (431/0); *0ph2, M. tentoriopharyngealis present (494/1)*

(*Macroxyela* + *Zorotypus*) (apomorphy-complex 2) (BS: 2)

genal rim equipped with irregularly distributed hairs (9/3); *epicranial (= coronal) suture (adults) absent (46/0)*; *frontal suture (adults) absent (47/0)*; *sitophore present (384/1)*; *0hy7, M. praementosalivaris anterior present (436/1)*; *single pair of salivary glands present (500/0)*; *0hy13, M. annularis salivarii present (510/1)*

(*Osmylus* + (*Schizodactylus* + Acercaria)) (apomorphy-complex 3) (BS: 2)

clypeoloral cleft present (54/1); origin of 0hy2, M. tentorioralis on tentorium (430/0); precibarium absent (474/0); *0bu5, M. tentoriobuccalis anterior present (490/1)*

(*Schizodactylus* + Acercaria) (apomorphy-complex 4) (BS: 2)

paired dorsal cervical sclerites present (13/0); *ocelli absent (18/0)*; 0an4, M. tentorioscapalis medialis absent (154/0); *origin of extrinsic antennal muscles 0an1 and 0an2 on anterior tentorial arms (155/0)*; *0md4, M. hypopharyngomandibularis present (198/1)*; 0hy4, M. postoccipitalohypopharyngealis present (432/1); *0hy5, M. tentoriosuspensorialis absent (435/0)*; *0bux1, “M. frontobuccalis anterior secundus” present (492/1)*

Acercaria (apomorphy-complex 5) (BS: 14)

mandible with mesal indentation as recess for galea (172/1); articulation of lacinia internalized (214/1); lacinia stylet-like (215/1); *tip of lacinia with setae (218/1)*; lacinia detached from stipes (220/1); cardo absent (230/0); 0mx1, M. craniocardinalis absent (261/0); 0mx3, M. tentoriocardinalis absent (264/0); 0mx9, M. stipitopalpalis medialis absent (272/0); *0mx15, M. palpopalpalis maxillae quartus absent (277/0)*; *presence of single glossa (302/1)*;

postmentum not subdivided in submentum and mentum (309/0); labial palpus composed of single segment (318/2); *0la17, M. palpopalpalis labii secundus absent (341/0)*; *sitophore present (384/1)*; *tormae absent (453/0)*; ventral orientation of floor of foodpump (473/0); *0bu6, M. tentoriobuccalis posterior absent (491/0)*

Psocoptera (apomorphy-complex 6) (BS: 3)

clypeal subdivision into small stripe-like anteclypeus and moderately bulging postclypeus (in comparison to Cicadomorpha) (35/3); *epistomal ridge present (48/1)*; antennal rupture-facilitating device (Seeger 1975) (143/1); *0an3, M. tentorioscapalis lateralis present (153/1)*; trifurcated tip of lacinia (217/2); *0mx10, M. stipitopalpalis internus present (273/1)*; *median cone (bar) located between bases of oral hypopharyngeal arms (397/1)*; *swollen paired ovoid sclerites present (404/1)*; *paired filamentous ligaments connecting sitophore and ovoid sclerite present (407/1)*; *water vapor uptake facility present (420/1)*; *mortar and pestle apparatus present (421/1)*

Troctomorpha (apomorphy-complex 7) (BS: 3)

head capsule dorso-ventrally flattened (5/1); compound eye composed of 7 to 8 ommatidia (24/0); *posterior tentorial arm longer than width of corpotentorium (width between both arms if corpotentorium absent) (109/1)*; *orientation of hypopharynx cranio-caudal (388/1)*; *distinct bent of pharynx absent (483/0)*; *protocerebral part folded backwards above subesophagealganglion (515/1)*

(Trogiomorpha + Psocomorpha) (apomorphy-complex 8) (BS: 8)

clypeal suture present (37/1); *origin of extrinsic antennal muscles 0an1 and 0an2 on anterior and dorsal tentorial arms (155/4)*; *mesal side of galea glabrous (247/0)*; *origin of 0mx2, M. craniolacinialis on vertex (263/0)*; *Y-shaped sclerite connected with prementum for support of glossa present (303/1*); oral hypopharyngeal arm shorter than sitophore (or body of hypopharynx) (396/1); *lingua present (423/1)*; *superlingua present (424/1)*; *0hy7, M. praementosalivaris anterior present (436/1)*

Psocomorpha (apomorphy-complex 9) (BS: 5)

Idvm1, M. cervico-occipitalis anterior present (73/1); *Ipcm1, M. procoxa-cervicalis present (88/1)*; antennal rupture-facilitating device non-functional or absent (144/1); *tip of lacinia bi-*

furcated (217/1); *0mx7, M. stipitogalealis absent (269/0)*; conical lobe between paraglossae present as extension of median part of glossa (307/1); *vertical orientation of floor of foodpump (473/2)*

(*Stenopsocus* + Psocotae) (apomorphy complex 10) (BS: 2)

ocelli present (18/1); *posterior tentorial arm longer than width of corpotentorium (minimal width between both arms if corpotentorium absent) (109/1)*; *molar teeth absent (186/0)*

Psocotae (apomorphy complex 11) (BS: 2)

cuticular condyles of postocciput present (32/1); *antennifer present (123/1)*

Acercaria excl. Psocoptera or (Condylognatha + Phthiraptera) (apomorphy-complex 12) (BS: 3)

lpcm2, M. procoxa-cervicalis transversalis absent (89/0); insertion of 0md4, M. hypopharyngomandibularis restricted to posterior outer edge of mandibular cavity (199/1); 0mx12, M. palpopalpalis maxillae primus absent (274/0); *0mx14, M. palpopalpalis maxillae tertius absent (276/0)*; contraction of labium during initialization of feeding (326/1); *0la16, M. palpopalpalis labii primus absent (340/0)*; *0bu5, M. tentoriobuccalis anterior absent (490/0)*

Phthiraptera (apomorphy-complex 13) (BS: 5)

head capsule dorso-ventrally flattened (5/1); compound eye composed of two ommatidia (24/2); *subdivision of clypeus absent* (*34/0)*; *gula present (41/1)*; *origin of labium on anterior part of head capsule or anterior to gula (288/0)*; *cranio-caudal orientation of hypopharynx (388/1)*; *0hy8, M. praementosalivaris posterior absent (437/0)*; *distinct bent of pharynx absent (483/0)*; *0ph3, M. postoccipitopharyngealis present (495/1)*; *protocerebral part folded backwards above subesophagealganglion (515/1)*

Amblycera (apomorphy-complex 14) (BS: 5)

antenna folded below head, held in groove (formed by gena) (119/1); *antenna composed of 4 segments (126/1)*; distal antennomeres (3 + 4) resembling a cupula enclosing an acorn (128/1); *0an3, M. tentorioscapalis lateralis present (153/1)*; stipes fused with ventral head capsule and labium (235/1); presence of 0mxx2, “M. palpopalpalis maxillae secundus

secundus" (279/1); *paired filamentous ligaments connecting sitophore and ovoid sclerite present (407/1)*; *tormae present (453/1)*

Amblycera excl. *Trochiloecetes* (apomorphy-complex 15) (BS: 2)

posterior tentorial arm longer than width of corpotentorium (or minimal width between both arms) (109/1); origin of 0mx8, M. stipitopalpalis externus on head capsule (271/2); *swollen paired ovoid sclerites present (404/1)*; *distal region of hypopharynx equipped with thorns or bristles (422/1)*; *epipharyngeal sclerite not developed as pistill of "mortar and pestle" apparatus (456/0)*; *ring muscle layer of foodpump/prepharynx absent (484/0)*; *0bu5, M. tentoriobuccalis anterior present (490/1)*

Menoponidae (apomorphy-complex 16) (BS: 1)

Ipcm2, M. procoxa-cervicalis transversalis present (89/1); *Clypealligament of Haub (1967) (connecting roof of head capsule with anterior tentorial arm/Laciniadrüse) present (118/1)*

(*Myrsidea* + *Pseudomenopon*) (apomorphy-complex 17) (BS: 3)

0md6, M. tentoriomandibularis lateralis inferior present (201/1); *sitophore with fenestration(s) (opening for cibarial sense organ) covered with membranes (385/1)*; presence of 0hy1, M. frontooralis including "Ligament of Denis" (running from laterodorsal side of clypeus to oral arms of hypopharynx) (428/1); *0hy5, M. tentoriosuspensorialis present (435/1)*; *0hyx2, "tentorial ligament" present (443/1)*; *tormae absent (453/0)*; *0bu6, M. tentoriobuccalis posterior present (491/1)*

(Ischnocera + (Anoplura + Rhynchophthirina)) (apomorphy-complex 18) (BS: 5)

presence of 2 ventral and 2 dorsal postoccipital condyles *(or unpaired apodeme) (33/1)*; *Idlm2, M. pronoto-occipitalis absent (70/0)*; *Ivlm3, M. profurca-tentorialis absent (96/0)*; stipes not developed as well defined element (234/0); *mesal side of galea glabrous (247/0)*; *palpus maxillaris (maxillary palp) absent (254/0)*; *0mx8, M. stipitopalpalis externus absent (270/0)*

Ischnocera (apomorphy-complex 19) (BS: 7)

pulvinus present (50/1); *"ventrale Längsleisten" (Risler 1951) enclosing labium and gula present (58/1)*; presence of median rim on ventral side of head capsule for fixing hairs or feath-

ers, between mandibles and anterior margin of head (64/1); *posterior tentorial arm longer than width of corpotentorium (or minimal width between both arms) (109/1)*; *Clypealligament of Haub (1967) (connecting roof of head capsule with anterior tentorial arm/Laciniadrüse) present (118/1)*; antennal squama present (122/1); *lingua present (423/1)*; *superlingua present (424/1)*; *0hyx2, "tentorial ligament" present (443/1)*; *0phx1, "M. sitophori pharyngis" present (496/1)*

(*Bovicola* + *Columbicola*) (apomorphy-complex 20) (BS: 1)

swollen paired ovoid sclerites present (404/1); *paired filamentous ligaments connecting sitophore and ovoid sclerite present (407/1)*; *mortar and pestle apparatus present (421/1)*; *obturaculum present (522/1)*

(Anoplura + Rhynchophthirina) (apomorphy-complex 21) (BS: 9)

compound eye composed of single ommatidium (24/3); *cuticular condyles of postocciput present (32/1)*; *anterior tentorial pits absent (44/0)*; *epicranial (= coronal) suture (adults) present (46/1)*; *anterior tentorial arms absent (105/0)*; *corpotentorium/tentorial bar/tentorial bridge absent (112/0)*; presence of antennal pore organs (149/1); *origin of extrinsic antennal muscles 0an1 and 0an2 on head capsule (155/1)*; mandibles and maxillae shifted craniad, articulations at or anterior to level of hypopharyngeal tip (166/1); *mandible without mesal indentation as recess for galea (172/0)*; absence of 0mx6, M. stipitolacinialis (268/0); *glossa absent (301/0)*; *prementum not folded to form salivary canal (312/0)*; labrum equipped with teeth (369/1); "Mundvorraum" present (476/1)

Anoplura (apomorphy-complex 22) (BS: 18)

two postoccipital condyles present dorsally (33/0); salivary meatus completely closed (66/1); meatus oris present (67/1); *mandibular articulation internalized (160/1)*; mandible divided into globular to flattened ventral part and flattened to half-pipe-shaped dorsal region (168/3); mandibles used for transport of liquids (171/3); mesal incisivial parts of mandibles forming closed canal (179/1); *incisivi absent (183/0)*; labium fused with pleuro- and hypostomal margin of head capsule to "poche gnathale" (von Kéler 1966) or fused complex of labrum, clypeus, and labium (289/1); ventral labial piercing bristle present (313/1); limes labialis present (314/1); dorsal and ventral apodeme of ventral labial piercing bristle present (316/1); *labial palp absent (317/0)*; dorsal hypopharyngeal piercing bristle present (410/1); "dorsale Führungsrinne der Stechborsten" present (411/1); median salivary stylet present (413/1);

piercer sheath present (415/1); *0hy7, M. praementosalivaris anterior present (436/1)*; fulcrum on roof of haustellum present (458/1); *ring muscle layer of foodpump/prepharynx absent (484/0)*; *obturaculum present (522/1)*

(*Pediculus* + *Phthirus*) (apomorphy-complex 23) (BS: 2)

epistomal ridge present (48/1); *0hy12, M. hypopharyngosalivaris absent (440/0)*; *epipharyngeal sclerite absent (454/0)*; *0ph1, M. verticopharyngealis absent (493/0)*

(*Haematopinus* + *Hybophthirus*) (apomorphy-complex 24) (BS: 4)

"ventrale Längsleisten" (Risler 1951) enclosing labium and gula present (58/1); Lig4 of Tröster (1990a) present (102/1); Lig5 of Tröster (1990a) present (103/1); *Clypealligament of Haub (1967) (connecting roof of head capsule with anterior tentorial arm/Laciniadrüse) present (118/1)*; caudal region of galea fused with tip of dorsal hypopharynx (252/1); posterior arms of hypopharynx as guiding device for ventral part of hypopharynx (402/1); *swollen paired ovoid sclerites present (404/1); paired filamentous ligaments connecting sitophore and ovoid sclerite present (407/1)*; *0hy2, M. tentorioralis present (429/1)*

Condylognatha (apomorphy-complex 25) (BS: 21)

ocelli present (18/1); *foramen occipitale pantotrem (31/0); frontal suture (adults) absent (47/0);* pleurostomal ridge absent (59/0); mandible stylet-like (168/1); mandibles with piercing function (171/1); mandibular gnathal pouche present (193/1); *0md4, M. hypopharyngomandibularis absent (198/0)*; interlocked laciniae grooved to form one or two canal(s) (221/1); *galea absent (242/0)*; maxillary lever present (256/1); *0mx5, M. tentoriostipitalis posterior absent (266/0)*; *0mx7, M. stipitogalealis absent (269/0); 0la5, M. tentoriopraementalis absent (332/0);* labrum narrowed, triangular, tongue-shaped (368/1); hypopharynx not tongue-shaped (382/1); sitophore of hypopharynx developed as salivary pumping chamber (387/1); piston present (392/1); *oral arms of hypopharnyx absent (394/0); posterior arms of hypopharynx absent (398/0);* suspensorium elongated and wing-like (409/1); hypopharynx with grooves as guiding devices for mandibles/maxillae (419/1); *0hy1, M. frontooralis absent (427/0)*; inter-pharyngeal locking mechanism present (468/1); *precibarium, prepharynx (narrow canal situated between food canal of maxillae and cibarium sensu stricto*) *present (474/1); ring muscle layer of foodpump/prepharynx absent (484/0); salivary accessory duct with distinct bent (505/1)*

Thysanoptera (apomorphy-complex 26) (BS: 20)

head asymmetric (4/1); *clypeal suture present (37/1)*; *ltpm1, M. pleurocrista-occipitalis absent (86/0)*; *lpcm1, M. procoxa-cervicalis present (88/1)*; asymmetry of anterior tentorial arms (106/1); only left mandible functional (167/1); *protrusion of proximal part of mandible as long and slender apodeme or tendon (a) absent (178/0)*; distal region of stipes encircled by distal mesal wall of labrum (236/1); *origin of 0mx2, M. craniolacinialis on gena (263/3); 0mxx3, retractor of maxillary lever present (280/1); 0mxx5, protractor of maxillary lever present (283/1);* labrum forming sheath for mandible and maxillae (371/1); tip of labrum separated from remainder of labrum by membrane or ledge (372/1); hypopharynx equipped with additional wings (383/1); hypopharynx forms sclerotized ring on roof of salivarium (salivary pump), origin of membranous piston (390/1); latero-ventral protrusion of epipharynx fitting into grooves of lacina (470/1); sclerotized clasp separating pharynx from cibarium (482/1); *0bu1, M. clypeobuccalis absent (486/0)*; *0ph1, M. verticopharyngealis absent (493/0)*; *subesophagialganglion forming compact complex with brain (517/1)*

Tubulifera (apomorphy-complex 27) (BS: 10)

clypeoloral cleft absent (54/0); "Wangenspalt" (Mickoleit 1963) as lateral cleft of head capsule running from margin of postocciput to gena (57/1); laterocranial sclerotized connection of mandibular base with stipes present (176/1); *0md8, tentoriomandibularis medialis inferior present (203/1)*; origin of 0lb1, M. frontolabralis shifted to right side, one portion on clypeofrons, one on right rudiment of anterior tentorial arm (374/1); *0lbx2, "M. tentorioepipharyngealis" present (381/1)*; origin of 0hy4, M. postoccipitalohypopharyngealis on gena (433/1); *0ci1, M. clypeopalatalis absent (485/0)*; *2 pairs of salivary glands present (500/2)*; *0hy13, M. annularis salivarii present (510/1)*

Terebrantia (apomorphy-complex 28) (BS: 1)

anteclypeus or anterior region of clypeus membranous (36/1); "Antennenring" (Mickoleit 1963) present (129/1); only a part of mandibular base visible externally (161/1); *0la4, M. postoccipitopraementalis primus present (330/1); 0hy7, M. praementosalivaris anterior present (436/1)*

Aeolothripidae (apomorphy-complex 29) (BS: 7)

cuticular condyles of postocciput present (32/1); *cardo present (230/1)*; *0mx3, M. tentoriocardinalis present (264/1)*; *0mx9, M. stipitopalpalis medialis present (272/1)*; 0mxx4, "M. lacinio-mandibularis" present (282/1); presence of 5-segmented labial palp (318/0); *0la11, M. praementoparaglossalis present (336/1); 0bu3, M. frontobuccalis posterior absent (488/0)*

Hemiptera (apomorphy-complex 30) (BS: 13)

first pair of lateral cervical sclerites (articulation with head capsule) absent (10/0); 2 ocelli (19/1); mandibular plates (lora) present (42/1); *mandibular articulation internalized (160/1)*; condylus of mandibular base absent (162/0); symmetry of mandibles (170/0); mandible or mandibular stylet encircling lacinia (175/1); barb-like structures at distal mandibular tip present (182/1); mandibular lever present (189/1); *palpus maxillaris absent (254/0); 0mx8, M. stipitopalpalis externus absent (270/0);* labium forms tube-like sheath for mandibles and lacinae (291/1); prementum not folded to form salivary canal *(312/0)*; *labial palp absent (317/0)*; *0la14, M. praementopalpalis externus absent (339/0)*; *labrum immobilized (367/0)*; *0lb1, M. frontolabralis absent (373/0)*; *0lb2, M. frontoepipharyngalis absent (375/0)*; *0lb5, M. labroepipharyngealis absent (378/0)*; salivary pumping chamber or salivarium only formed by hypopharynx (389/0); opening of salivarium or pumping chamber between maxillary stylets (391/0); *0hy4, M. postoccipitalohypopharyngealis absent (432/0)*; *0bux1, "M. frontobuccalis anterior secundus" absent (492/0)*; *0st2, M. longitudinalis stomodaei absent (498/0)*; *vesicular structure of accessory gland (504/0)*

Heteroptera (apomorphy-complex 31) (BS: 7)

gula present (41/1); *anterior tentorial pits absent (44/0)*; *Idvm9, M. profurca-occipitalis present (79/1)*; *anterior tentorial arms absent (105/0)*; *antenna composed of 4 segments (126/1)*; *origin of extrinsic antennal muscles 0an1 and 0an2 on head capsule (155/1)*; *0md6, M. tentoriomandibularis lateralis inferior absent (201/0)*; *origin of labium on anterior part of head capsule (288/0)*; *principal salivary gland distinctly bi-lobed (502/1)*

Heteroptera excl. *Corixa* (apomorphy-complex 32) (BS: 3)

bucculae present (40/1); *intercalary sclerites between antennomeres 2 and 3 (137/1);* intercalary sclerites ("intraflagelloid, if") between antennomeres 3 and 4 (139/1); *0mdx1, mandi-*

bular retractor present (204/1); *cranio-caudal orientation of hypopharynx (including pumping chamber) (388/1)*; *pharynx without distinct bent (483/0)*; *subesophagial ganglion forms compact complex with brain (517/1)*

Heteroptera excl. *Corixa*, *Dysdercus* (apomorphy-complex 33) (BS: 1)

epistomal ridge present (48/1); *0mdx3, protractor of mandibular lever present (207/1)*

Heteroptera excl. *Corixa*, *Dysdercus*, *Triatoma* (apomorphy-complex 34) (BS: 1)

mandibular lever formed as acute triangle with arm attached to mandible elongated (190/1); *tube-like labium composed of 3 segments (292/2)*; *0lax1, labial abductor present (342/1)*

(*Cryptostemma* + Schizopteridae + (*Hypsipteryx* + (*Systelloderes* + (*Gerris* + *Hydrometra*)))) (apomorphy-complex 35) (BS: 2)

ocelli absent (18/0); type pf(IV) of preflagelloid (Zrzavý 1990) present (138/2); *0ph1, M. verticopharyngealis absent (493/0)*; *principal salivary gland indistinctly bi-lobed (502/0)*

(*Hypsipteryx* + (*Systelloderes* + (*Gerris* + *Hydrometra*))) (apomorphy-complex 36) (BS: 1)

bucculae absent (40/0); *genal suture present (56/1)*

(*Systelloderes* + (*Gerris* + *Hydrometra*)) (apomorphy-complex 37) (BS: 2)

pf(I)-type of preflagelloid/prebasiflagellite (Zrzavý, 1990) (138/1); *tripartite apex of labial rostrum or closing lid at distal end of terminal labial segment present (298/1)*

Gerromorpha (apomorphy-complex 38) (BS: 2)

cephalic trichobothria present (60/1); tip of lacinia equipped with setae *(218/1)*; *maxillary lever absent (256/0)*; *principal salivary gland distinctly bi-lobed (502/1)*

(*Saldula* + Nepomorpha) (apomorphy-complex 39) (BS: 2)

2 ventral and 2 dorsal postoccipital condyles present (33/1); *frontal suture (adults) present (47/1)*; *suspensory plate present (300/1)*; *epipharyngeal triturating devices present (471/1)*; *0bu5, M. tentoriobuccalis anterior present (490/1)*

Nepomorpha (apomorphy-complex 40) (BS: 3)

antenna folded below head, held in groove (formed by gena) (119/1); *origin of antennae below eyes (120/1)*; intercalary sclerites between antennomeres 3 and 4 absent *(139/0)*; *tip of lacinia with setae (218/1)*; *labial intercalary sclerites between 3rd and 4th labial segment of tube-like labium present (293/1)*; *tripartite apex of labial rostrum or closing lid at distal end of terminal labial segment present (298/1)*

Nepomorpha excl. *Ochterus*, *Gelastocoris* (apomorphy-complex 41) (BS: 2)

ocelli absent (18/0); *mandibular lever formed as acute triangle with arm attached to mandible elongated and caudally directed (190/2)*; *0mdx3, protractor of mandibular lever absent (207/0)*; *maxillary lever absent (256/0)*; *subesophageal ganglion or subesophageal ganglion-brain-complex fused with prothoracic ganglion (518/1)*

Hemiptera excl. Heteroptera (apomorphy-complex 42) (BS: 1)

ldvmx1, “M. pronoto-tentorialis primus” present (80/1); *origin of 0mx2, M. craniolacinialis on the vertex (263/0); capable of producing salivary sheaths (507/1)*

Sternorrhyncha (apomorphy-complex 43) (BS: 2)

posterior tentorial arm longer than width of corpotentorium (109/1); 0an4, *M. tentorioscapalis medialis present (154/1)*; *protrusion of proximal part of mandible as long and slender apodeme or tendon (a) absent (178/0)*; *two dendrites per mandibular dendritic canal (181/0)*; *0mdx2, mandibular retractor absent (206/0)*; *0ph1, M. verticopharyngealis absent (493/0)*; *salivary accessory duct without distinct bent (505/0)*

Aleyrodoidea (apomorphy-complex 44) (BS: 3)

distinct division of compound eye into 2 subunits (23/1); *position of point C (articulation point of mandibular lever with cranium or dorsal end of loromaxillary cleft separating maxillary plate from lorum) located near level of anterior tentorial pits or compound eyes (63/0)*; 0mxx6, “M. tentorio-lacinialis” present (284/1); *0lax1, labial abductor present (342/1)*; *0lax14, labial abductor present (356/1)*; *0hyx4, “M. hypopharyngo salivaris secundus” present (446/1)*

Sternorrhyncha excl. **Aleyrodoidea** (apomorphy-complex 45) (BS: 4)

presence of 3 ocelli (19/0); *clypeal suture present (37/1)*; *epistomal ridge present (48/1)*; insertion of Idvm4, M. pronoto-cervicalis lateralis on posterior tentorial arm (84/1); *0mdx3, protractor of mandibular lever present (207/1)*; *origin of 0mx2, M. craniolacinialis on posterior tentorial arm (263/1)*; *bar-shaped and unpaired apodeme of 2nd labial segment (also applicable if 1st segment reduced) absent (299/0)*; *0lax2, labial adductor absent (343/0)*; *origin of 0lax14 on the cranium (357/1)*; *principal salivary gland aciniform (506/0)*

(*Aphis* + *Dactylosphaera*) (apomorphy-complex 46) (BS: 7)

Idlm2, M. pronoto-occipitalis absent (70/0); Idvm4, M. pronoto-cervicalis lateralis absent (76/0); 0an3, M. tentorioscapalis lateralis present (153/1); locked maxillary stylets compressed laterally in cross-section (226/1); 0lax5, labial adductor present (347/1); 0lax6, labial adductor present (348/1); 0lax8, transvere labial muscle present (350/1); *0lax11, basal labial muscle present (353/1); 0hyx4, “M. hypopharyngo salivaris secundus” present (446/1)*; 0hyx5, “M. hypopharyngo salivaris tertius” present (447/1); 0hyx7, “M. hypopharyngo salivaris quintus” present (449/1); *0bu5, M. tentoriobuccalis anterior present (490/1)*

(Coccoidea + Psylloidea) (apomorphy-complex 47) (BS: 2)

Idvmx2, “M. pronoto-genalis” present (81/1); mandibular and maxillary feeding stylets forming loop posteriorly in lateral view and resting position (187/2); crumena present (324/1); *0lax10, labial transversal muscle absent (352/0)*; 0lax12, muscle of labial crumena present (354/1)

Coccoidea (apomorphy-complex 48) (BS: 8)

sclerotization of head capsule incomplete (i.a. vertex, frons and genae membranous) (7/1); *ocelli absent (18/0)*; *compound eye composed of single ommatidium (24/3)*; *Idvm6, M. pronoto-cervicalis medialis present (78/1)*; *Itpm1, M. pleurocrista-occipitalis absent (86/0)*; *0mdx2, mandibular retractor present (206/1)*; *maxillary lever connected to hypopharyngeal wing or hypopharynx (257/0)*; *maxillary lever without muscle attachment (258/0)*; *0lax11, basal labial muscle present (353/1)*; 0lax13, basal labial muscle present (355/1)

Psylloidea (apomorphy-complex 49) (BS: 2)

cone-shaped frontal protrusions present (28/1); foramen occipitale in semi-dorsal position (30/2); *clypeal suture absent (37/0)*; *frontal suture (adults) present (47/1); mandibular lever absent (189/0)*; *0mdx4, protractor of mandibular lever absent (208/0);* procoxae covering basal part of labium, labium moved indirectly by prosternal movement or "partial accretion of bottom labium with ventral prothorax" (Drohojowska 2009) (290/1)

(*Psylla* + *Cacopsylla*) (apomorphy-complex 50) (BS: 9)

posterior tentorial pits absent (45/0); *genal suture absent (56/0)*; *Idvm9, M. profurca-occipitalis present (79/1)*; *locked maxillary stylets laterally compressed in cross-section (226/1)*; *tube-like labium composed of three segments (292/1)*; *0lax3, labial adductor absent (345/0)*; *0lax9, labial transverse muscle absent (351/0)*; *origin of 0hy12, M. hypopharyngosalivaris on corpotentorium (441/2)*; *0hyx4, "M. hypopharyngo salivaris secundus" present (446/1)*; *0bu5, M. tentoriobuccalis anterior present (490/1)*

((Fulgoromorpha + Coleorrhyncha) + Cicadomorpha) (apomorphy-complex 51) (BS: 1)

Idvm4, M. pronoto-cervicalis lateralis absent (76/0); *origin of 0lax2 on hypopharynx (344/0)*; *bark cell layer absent (521/0)*

(Fulgoromorpha + Coleorrhyncha) (apomorphy-complex 52) (BS: 1)

epistomal ridge present (48/1); *antennal origin below eyes (120/1)*; *maxillary lever without muscle attachment (258/0)*

Fulgoromorpha (apomorphy-complex 53) (BS: 1)

anterior tentorial pits absent (44/0); swollen bulbous pedicellus (at least twice as broad as scapus) (125/1); *0md6, M. tentoriomandibularis lateralis inferior absent (201/0)*

Coleorrhyncha (apomorphy-complex 54) (BS: 5)

head triangular with tapering tip caudally (2/1); anterior portion of head dorso-ventrally flattened compared to posterior cephalic region (6/1); areolae (thin fenestrations of head capsule) present (8/1); foramen occipitale in dorsal position (30/1); *antenna folded below head, held in groove (formed by the gena) (119/1)*

(*Pantinia* + (*Hackeriella* + *Hemiodoecus*)) (apomorphy-complex 55) (BS: 1)

ocelli absent (18/0)

(*Hackeriella* + *Hemiodoecus*) no apomorphies identified by NONA

Cicadomorpha (apomorphy-complex 56) (BS: 4)

antennal ledge present (121/1); origin of extrinsic antennal muscles 0an1 and 0an2 on dorsal tentorial arms (155/2); *three dendrites per mandibular dendritic canal (181/1); 0mxx3, retractor of maxillary lever present (280/1)*

(*Philaenus* + (Membracoidea + Cicadoidea)) (apomorphy-complex 57) (BS: 2)

clypeal suture present (37/1); *position of point C (articulation point of mandibular lever with head capsule or dorsal end of loromaxillary cleft separating maxillary plate from lorum) near level of anterior tentorial pits or compound eyes (63/0)*; *0mdx1, mandibular retractor present (204/1)*; *0bu5, M. tentoriobuccalis anterior present (490/1); 0ph2, M. tentoriopharyngealis present (494/1)*; *0ph3, M. postoccipitopharyngealis present (495/1)*

(Membracoidea + Cicadoidea) (apomorphy-complex 58) (BS: 2)

0an8, M. intraflagellaris (primus) present (158/1); 0anx1, “M. intraflagellaris secundus” *present (159/1)*

Cicadoidea (apomorphy-complex 59) (BS: 1)

first pair of lateral cervical sclerites (articulation with head capsule) present (10/1); *3 ocelli (19/0)*; *frontal suture (adults) present (47/1)*

Membracoidea (apomorphy-complex 60) (BS: 3)

cuticular postoccipital condyles present (32/1); *anterior tentorial arms not fused with corpotentorium (107/0)*; *maxillary lever with attachment of protractors (259/1)*; *0mxx3, retractor of maxillary lever absent (280/0)*

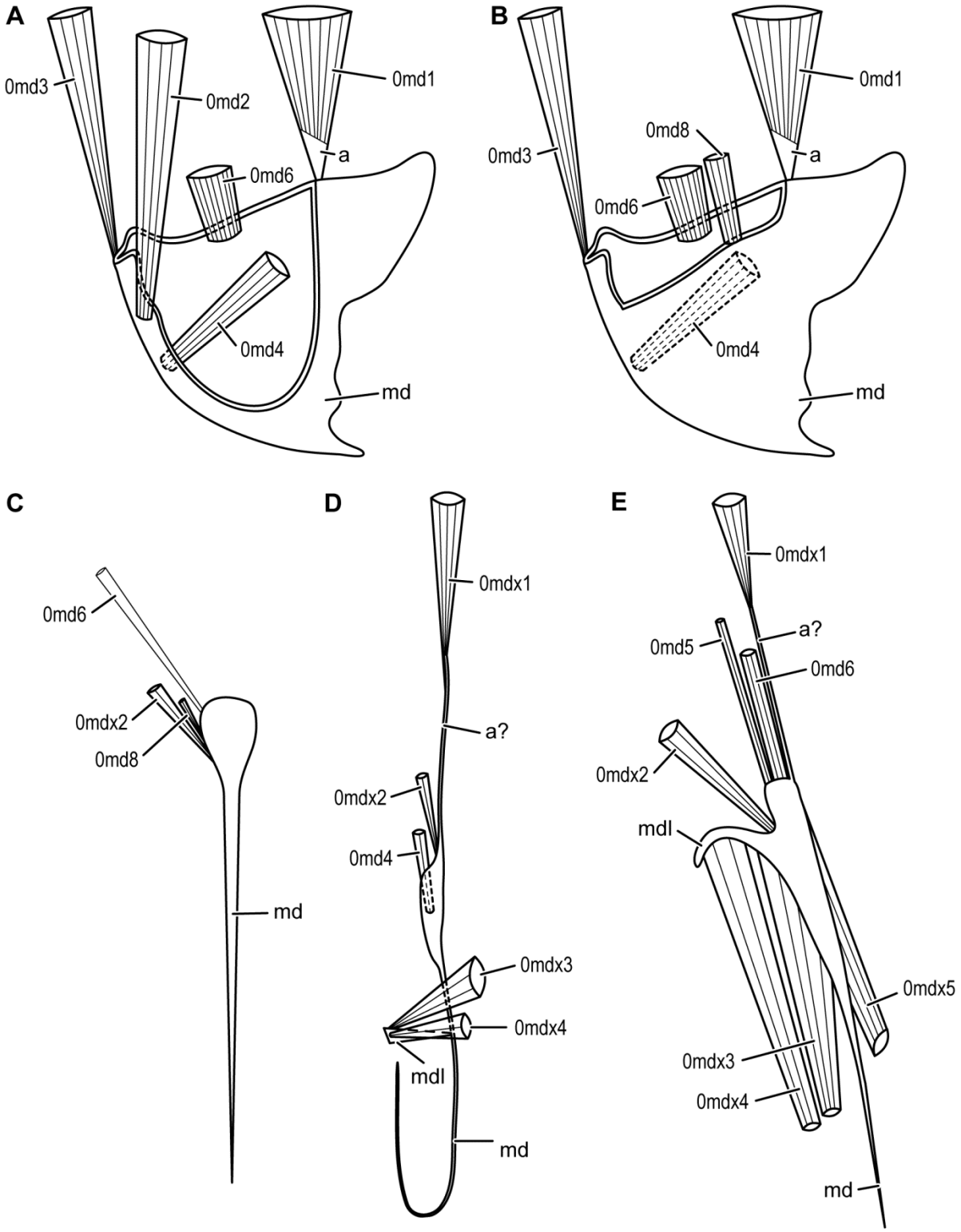


Figure 4. Overview of mandibular diversity within selected taxa of Acercaria, right mandible (left of *Phlaeothrips*) schematic, not true to scale, muscular nomenclature follows Wipfler et al. (2011) and Table 2. A: *Liposcelis* (Troctomorpha), Masumoto & Nagashima (1993) modified; B: *Cerobasis* (Trogiomorpha), Masumoto & Nagashima (1993) modified; C: *Phlaeothrips* (Thysanoptera), Mickoleit (1963) modified; D: *Systelloderes* (Heteroptera), Spangenberg et al. (2013b) modified; E: *Idiocerus* (Auchenorrhyncha), Arora & Singh (1962) modified. a, adductor tendon; md, mandible; mdl, mandibular lever.

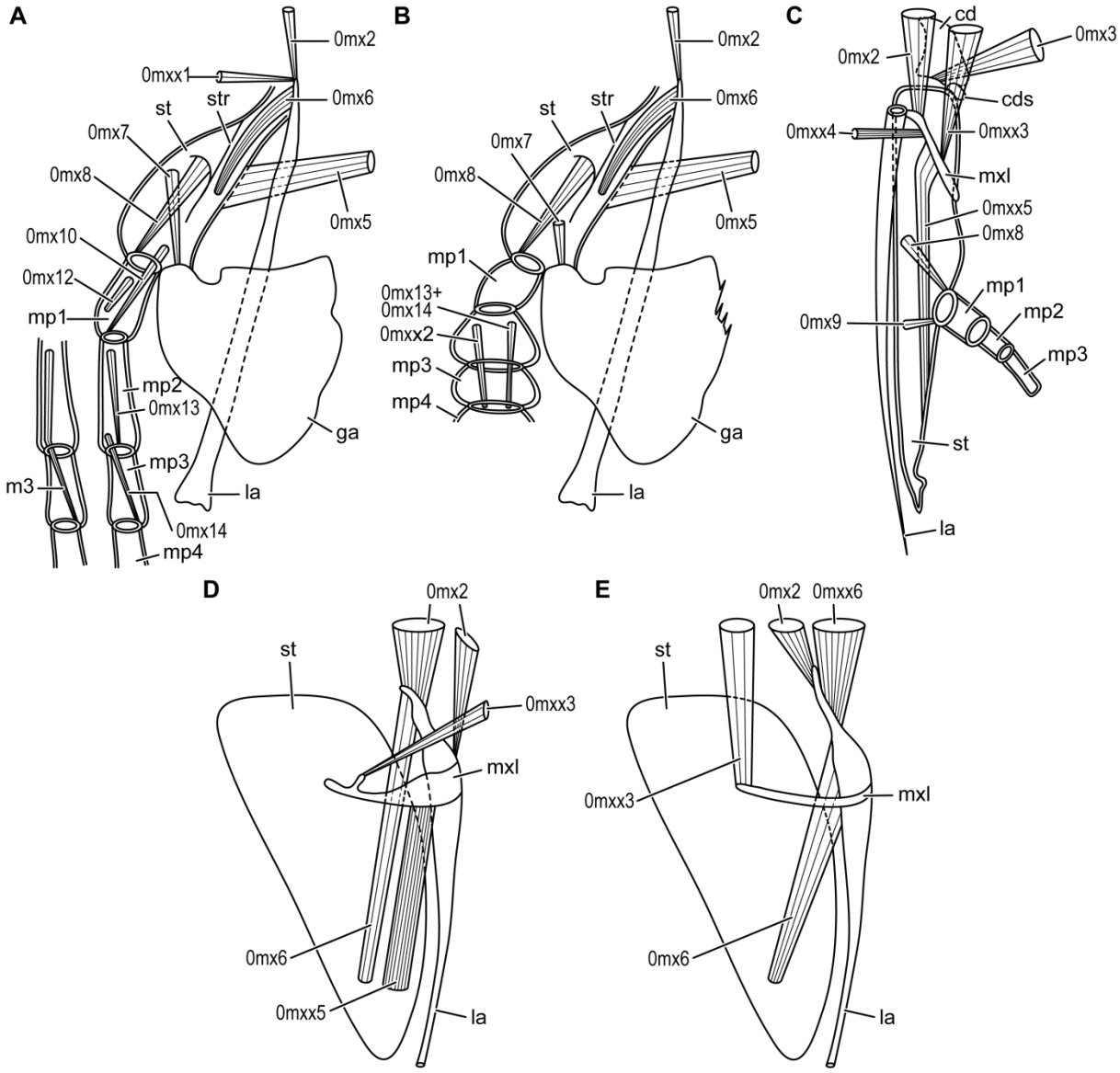
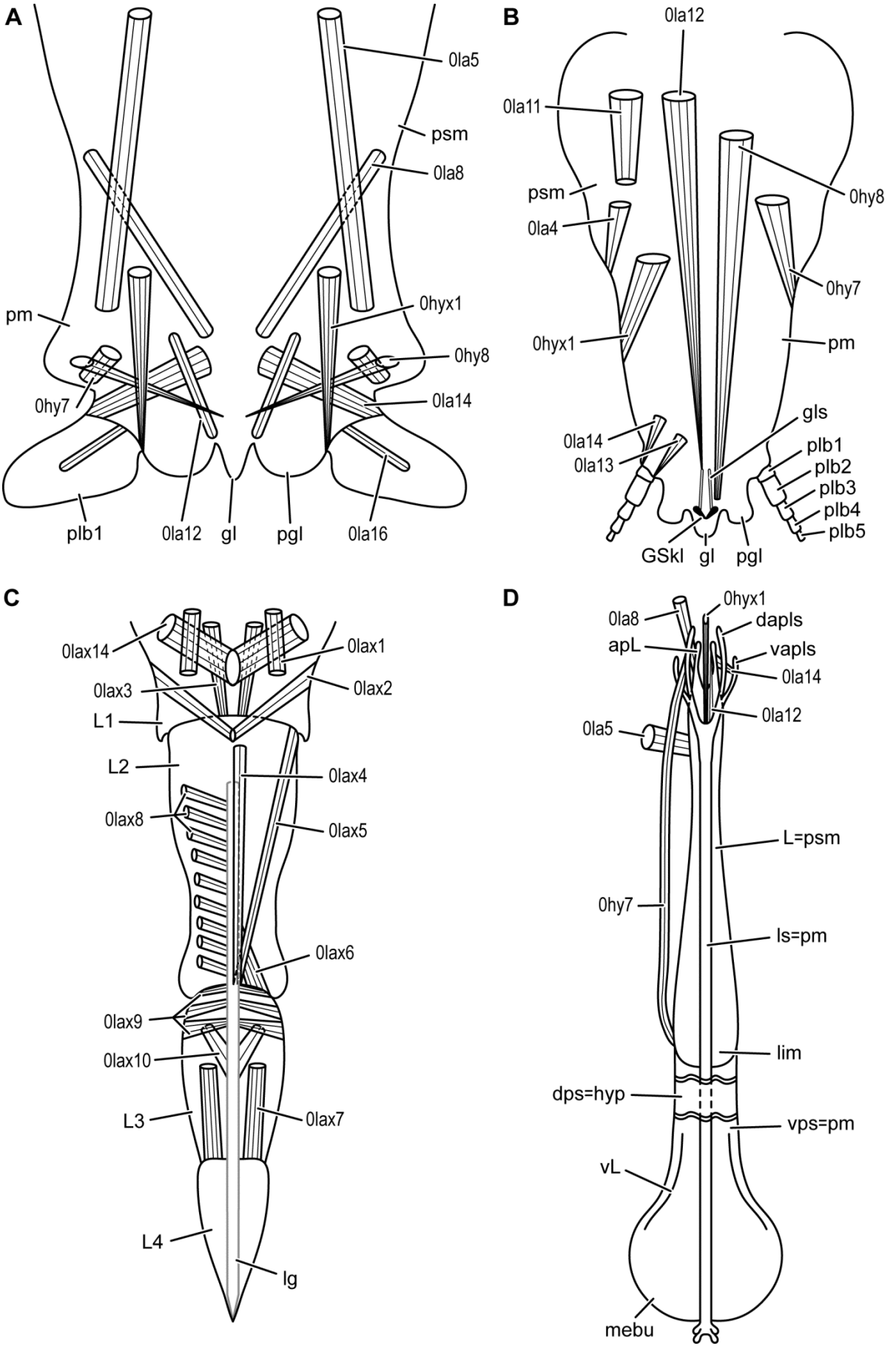


Figure 5. Overview of maxillary diversity including musculature within selected taxa of Acercaria, right maxilla (left of *Aeolothrips*) schematic, not true to scale, muscular nomenclature follows Wipfler et al. (2011) and Table 2. A: *Cerobasis* (Trogiomorpha), maxillary palp of *Stenopsocus* (Psocomorpha) as documented by Badonnel (1934) shown on the left, Masumoto & Nagashima (1993) modified; B: *Pseudomenopon* (Amblycera), Haub (1967) modified; C: *Aeolothrips* (Thysanoptera), Mickoleit (1963) and Moritz (1982b) modified; D: *Tibicina* (Auchenorrhyncha), Kramer (1950) modified; E: *Aleurodes* (Sternorrhyncha), Weber (1935) modified. ga, galea; la, lacinia; mp, maxillary palpomere with appropriate number; mxl, maxillary lever; st, stipes; str, stipital ridge.

Figure 6 (next page). Overview of labial diversity within selected taxa of Acercaria, schematic, not true to scale, muscular nomenclature follows Wipfler et al. (2011) and Table 2. A: *Stenopsocus* (Psocomorpha), frontal view, Badonnel (1934) modified; B: *Aeolothrips* (Thysanoptera), frontal view, Mickoleit (1963) modified; C: *Aphis* (Sternorrhyncha), frontal view, Weber (1928) modified; D: *Haematopinus* (Anoplura), dorsal view, Ramcke (1965) modified. apL, apodeme of L; dapls, dorsal apodeme of labial stylet; dps, dorsal part of anopluran piercer sheath, dorsal hypopharynx; gl, glossa; gls, sclerotized rod of glossa; GSkl, Gabelsklerit; L, sclerotized elongation of limes labialis and proximal ventral piercer sheath, part of postmentum; lim, limes labialis; ls, labial stylet, ventral bristle of Anoplura developed from prementum; mebu, membranous bulge; pgl, paraglossa; plb, labial palpomere with appropriate number; pm, prementum; psm, postmentum; vapls, ventral apodeme of labial stylet; vL, "ventrale Längsleisten" enclosing labium and gula; vps, ventral part of anopluran piercer sheath, ventral prementum.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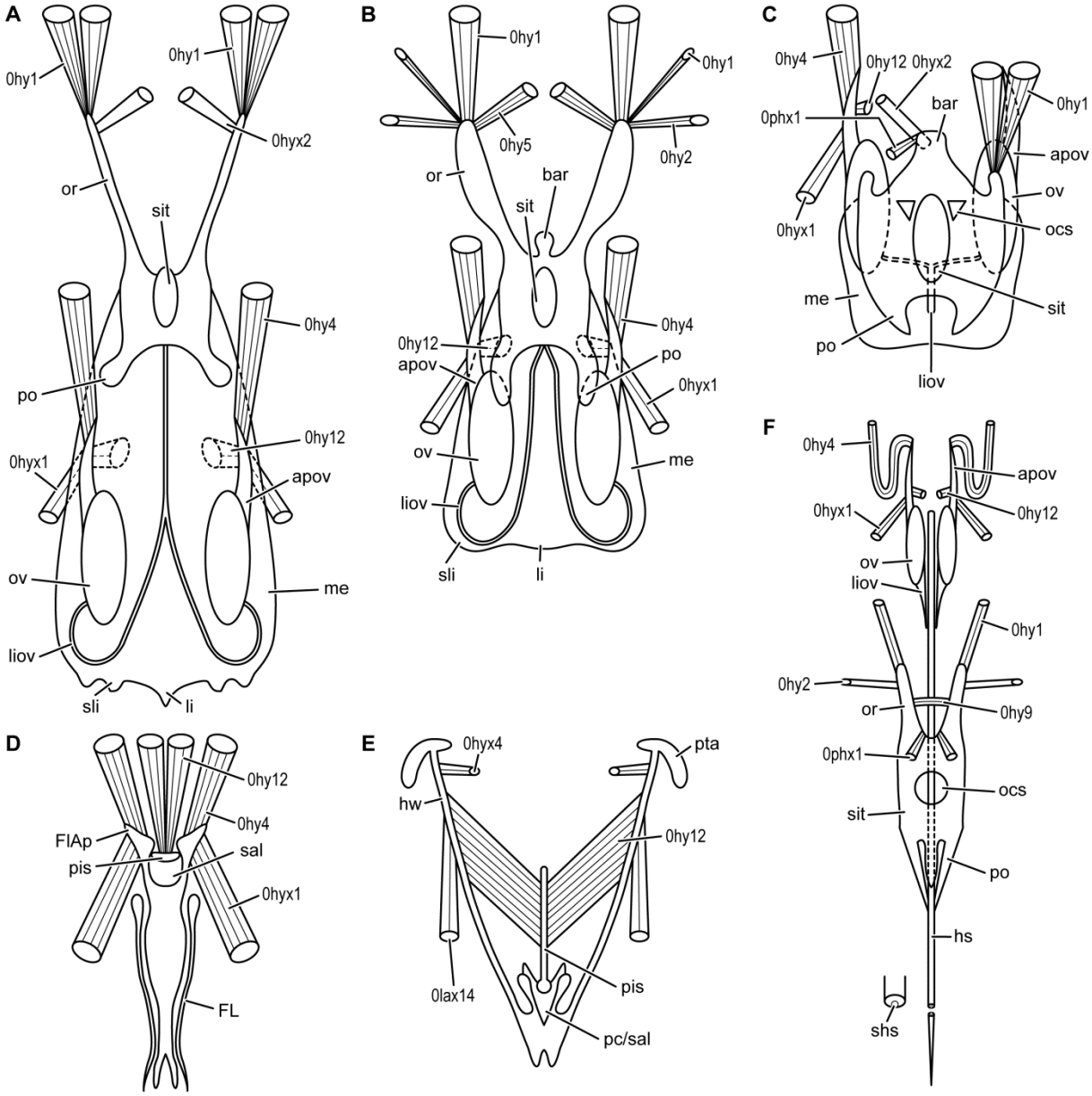
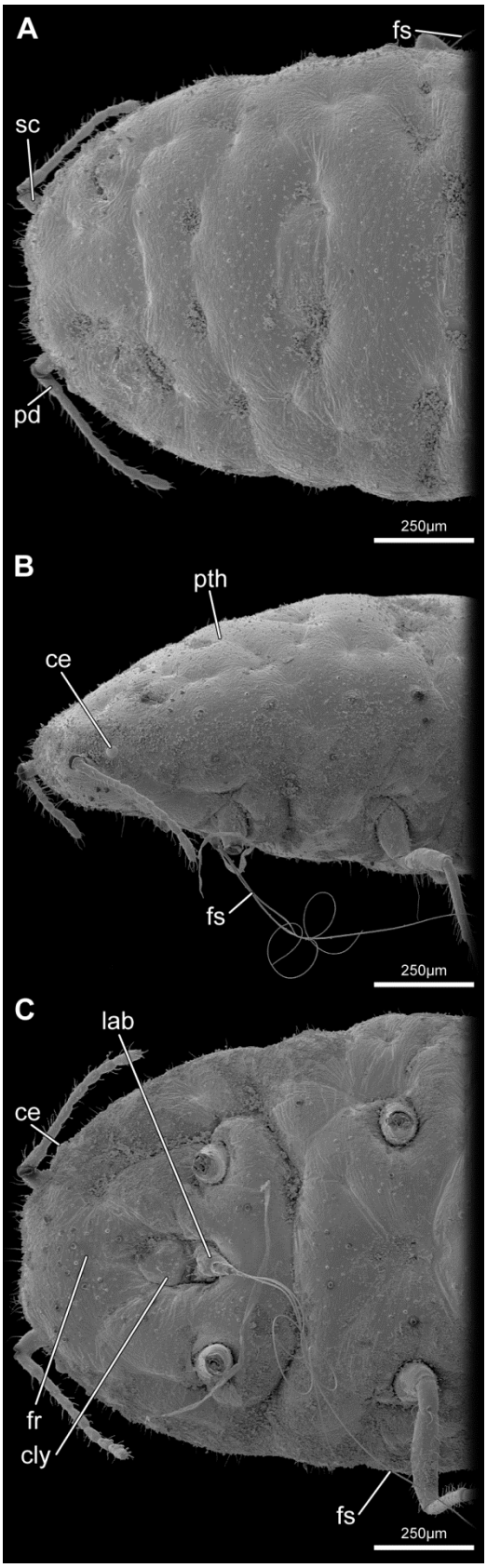


Figure 7. Overview of hypopharyngeal diversity within selected taxa of Acercaria, schematic, not true to scale, muscular nomenclature follows Wipfler et al. (2011) and Table 2. A: *Stenopsocus* (Psocomorpha), frontal view, Badonnel (1934) modified, 0md4 not labeled; B: *Cerobasis* (Trogiomorpha), frontal view, 0md4 not labeled; C: *Columbicola* (Ischnocera), dorsal view, 0md4 not labeled; D: *Aeolothrips* (Thysanoptera), frontal view, Mickoleit (1963) modified; E: *Hackeriella* (Coleorrhyncha), frontal view, Spangenberg et al. (2013a) modified; F: *Hybophthirus* (Anoplura), dorsal view, Tröster (1990a) modified, enlarged detail of median salivary stylet shown on the left. apov, posterior apodeme of ovoidal sclerite; bar, median bar located between bases of oral hypopharyngeal arms; FL, Führungsleiste der Lacinia; FIAP, Flügelapodem of hypopharynx; hs, hypopharyngeal stylet, dorsal bristle of Anoplura developed from ventral hypopharynx; hw, hypopharyngeal wing; li, lingua; liov, ligament connecting sitophore with ovoid sclerite; me, membrane; ocs, opening for cibarial sense organ; or, oral arm of hypopharynx; ov, ovoid sclerite of hypopharynx; pc, pumping chamber; pis, piston; po, posterior arm of hypopharynx according to Matsuda (1965p, p. 135 fig. 53B); pta, posterior tentorial arm; sal, salivarium; shs, salivary canal of hypopharyngeal sytlet = median salivary stylet; sit, sitophore of hypopharynx; sli, superlingua.



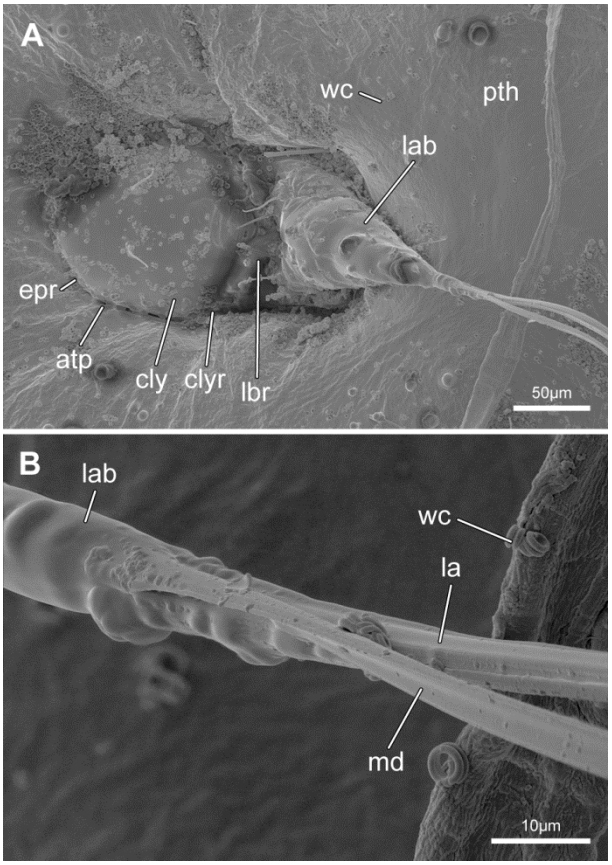


Figure 9. *Pseudococcus longispinus* (Sternorrhyncha), female, Scanning Electron Micrograph. A: ventral view of mouth field; B: detail of A. atp, anterior tentorial pit; cly, clypeus; clyr, clypeolabral ridge; epr, epistomal ridge; la, lacinia; lab, labium; lbr, labrum; md, mandible; pth, prothorax; wc, waxy crystal.

Figure 8. *Pseudococcus longispinus* (Sternorrhyncha), female, head and thorax, legs partly omitted, Scanning Electron Micrograph. A: dorsal view; B: lateral view; C: ventral view. ce, compound eye; cly, clypeus; fr, frons; fs, feeding stylets; lab, labium; pd, pedicellus; pth, prothorax; sc, scapus.

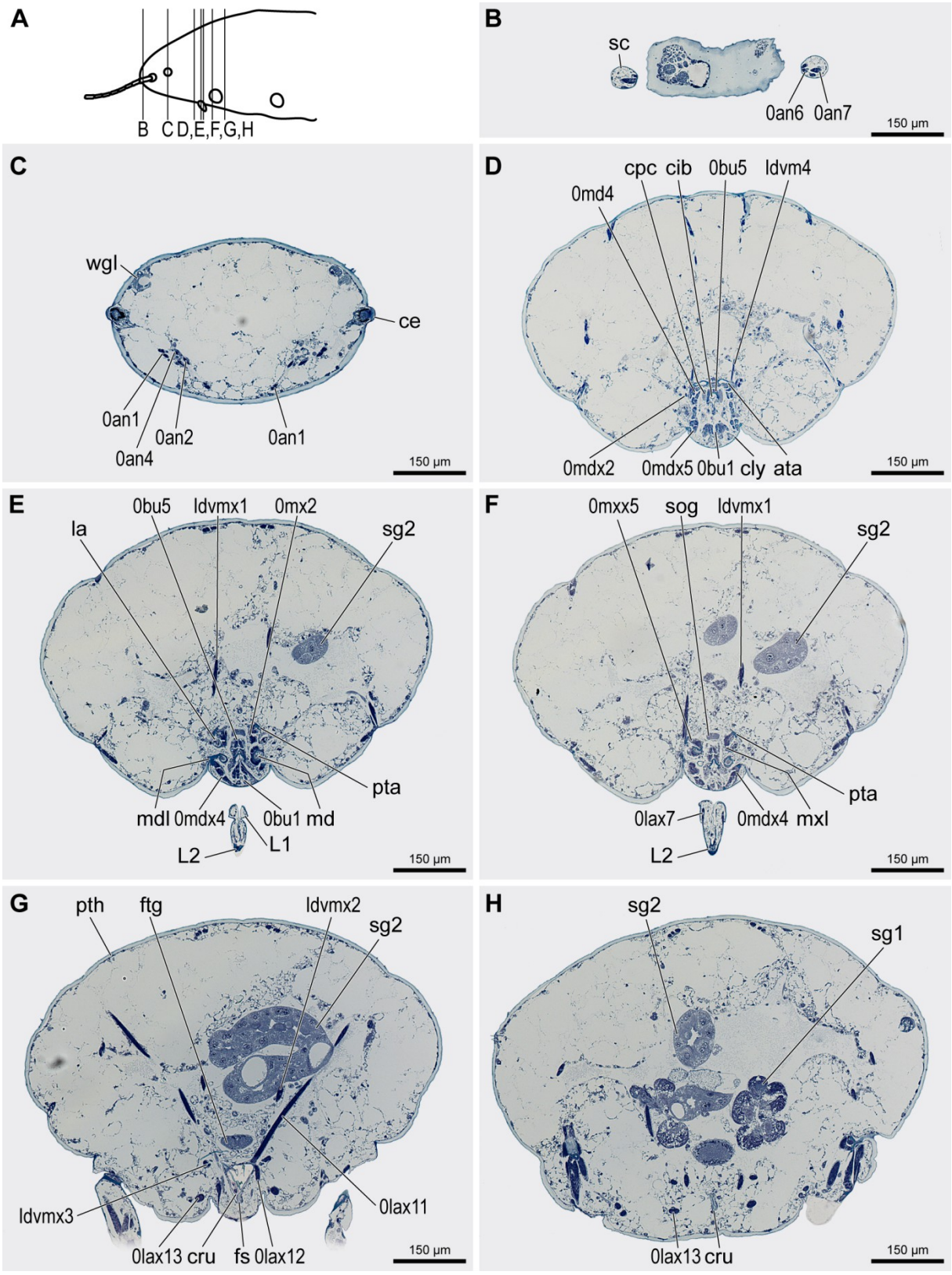


Figure 10. *P. longispinus*, female, head and thorax, cross sections. Muscular nomenclature follows Friedrich & Beutel (2008), Wipfler et al. (2011) and Table 2. A: head and thorax (legs omitted), schematic, lateral view showing planes of section of light micrographs B – H. ata, anterior tentorial arm; ce, compound eye; cib, cibarium; cly, clypeus; cpc, circumesophageal connective; cru, crumena; fs, feeding stylet; ftg, first thoracal ganglion; L1, L2, pre-apical and apical segment of labium; md, mandible; mdl, mandibular lever; mxl, maxillary lever; pta, posterior tentorial arm; pth, prothorax; sc, scapus; sg1, principal salivary gland; sg2, accessory salivary gland; sog, subesophageal ganglion; wgl, waxy gland.

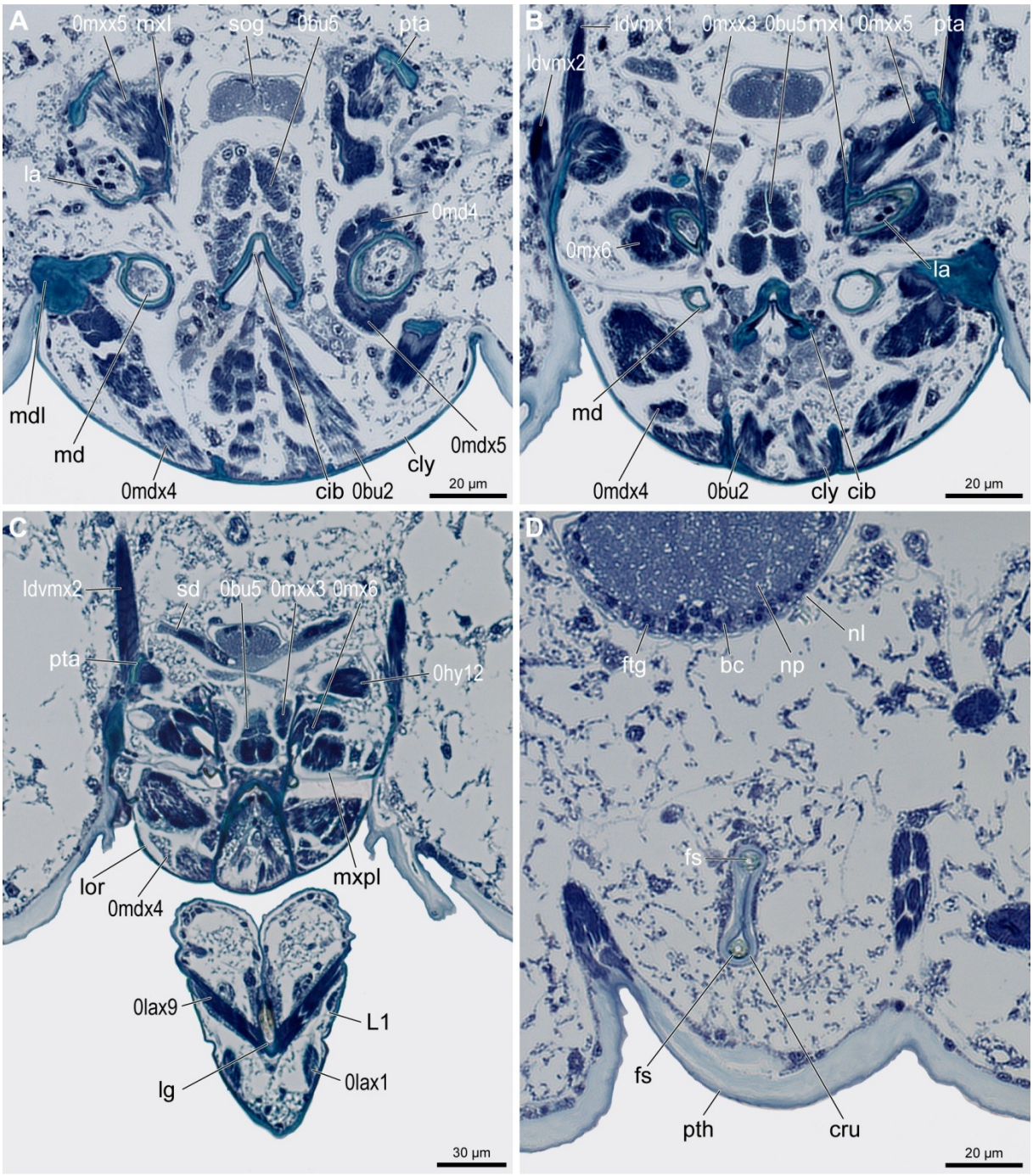


Figure 11. *Pseudococcus longispinus* (Sternorrhyncha), female, head and thorax, cross sections, details. Muscular nomenclature follows Friedrich & Beutel (2008), Wipfler et al. (2011) and Table 2. A: detail of Fig. 10E; B: plane of section 8 µm posterad to that of Fig. 10F; C: plane of section 13 µm posterad to that of Fig. 10F; D: plane of section 20 µm anterad to that of Fig. 10H. bc, bark cell; ce, compound eye; cib, ciarium; cly, clypeus; cru, crumena; fs, feeding stylets; ftg, first thoracal ganglion; L1, pre-apical segment of labium; la, lacinia; lor, lorum; md, mandible; mdl, mandibular lever; mxl, maxillary lever; mxpl, maxillary plate (stipes); nl, neural lamella; np, neuropil; pta, posterior tentorial arm; pth, prothorax; sd, common salivary duct.

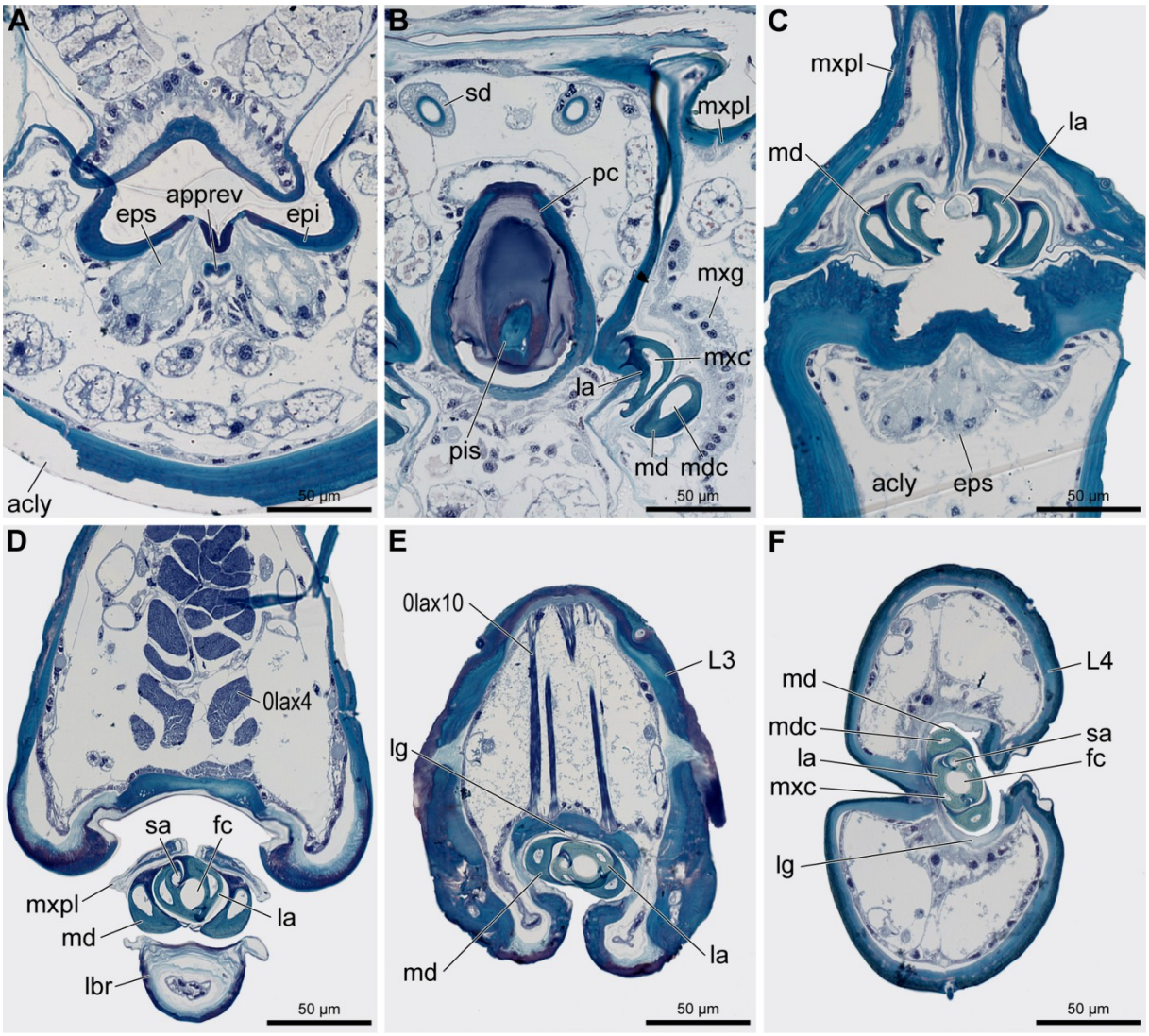


Figure 12. *Philaenus spumarius* (Cicadomorpha), unknown sex, details of cross sections from anterior (A) to posterior (F). F rotated 45° counterclockwise. Muscular nomenclature follows Table 2. acly, anteclypeus; apprev, apodeme of precibarial valve; epi, epipharynx; eps, epipharyngeal sense organ; fc, maxillary food canal; L2, L3, L4, 2nd, 3rd, and 4th labial segment; la, lacinia; lbr, labrum; md, mandible; mdc, mandibular dendritic canal (neural channel of Garzo et al. 2012); mxc, maxillary dendritic canal; mxg, maxillary gland; mxpl, maxillary plate (stipes); pc, pumping chamber; pis, piston; sa, maxillary salivary canal; sd, salivary duct.

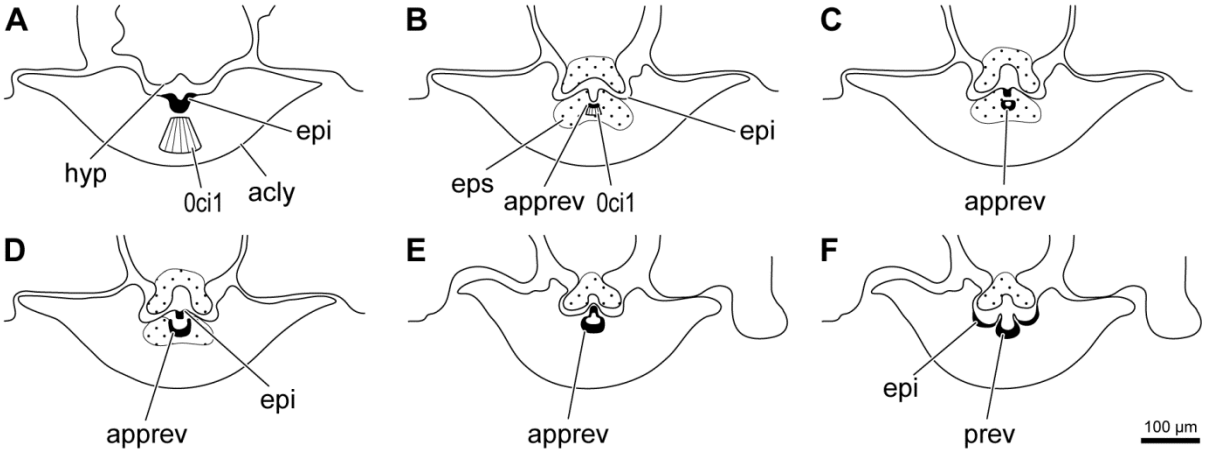


Figure 13. *Philaenus spumarius* (Cicadomorpha), unknown sex, precibarial valve schematic, cross sections from anterior (A) to posterior (F). Muscular nomenclature follows Wipfler et al. (2011). acly, anteclypeus; apprev, apodeme of precibarial valve; epi, epipharynx; eps, epipharyngeal sense organ; hyp, hypopharynx; prev, precibarial valve.

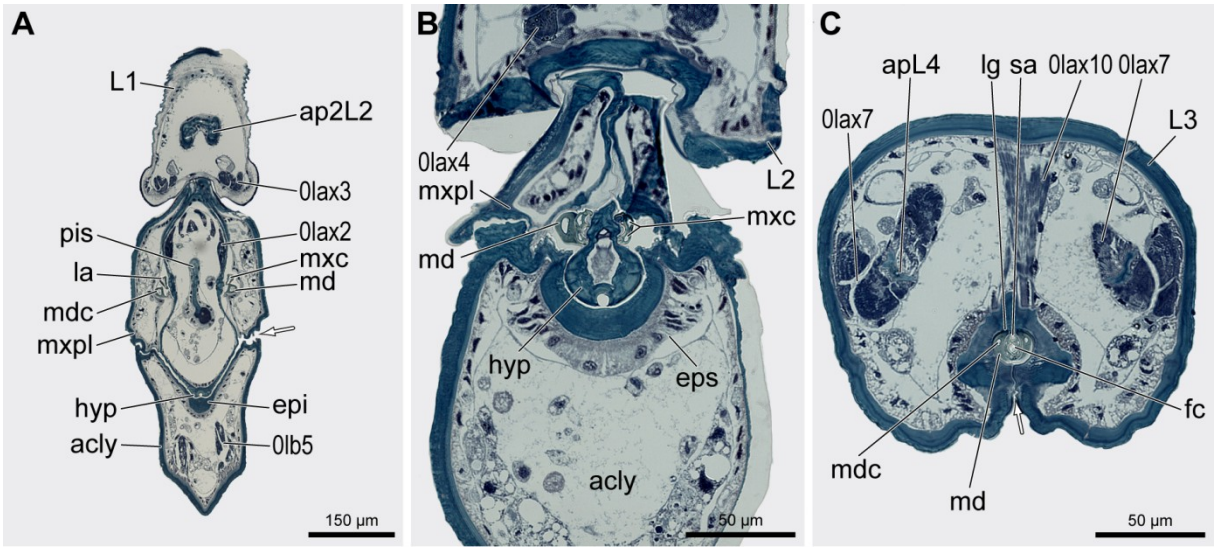


Figure 14. *Dictyophara europaea* (Fulgoromorpha), unknown sex, details of cross sections (different magnifications) of labium from proximal (A) to distal (C). Muscular nomenclature follows Wipfler et al. (2011) and Table 2. Arrows indicate linkage of anteclypeus with maxillary plates (A) and linkage of edges of labial groove (C), respectively. acly, anteclypeus; ap2L2, unpaired apodeme of 2nd labial segment; apL4, apodeme of 4th labial segment; epi, epipharynx; eps, epipharyngeal sense organ; fc, maxillary food canal; hyp, hypopharynx; L1, L2, L3, 1st, 2nd, 3rd labial segment; la, lacinia; lg, labial groove; md, mandible; mdc, mandibular dendritic canal; mxc, maxillary dendritic canal; pis, piston; sa, maxillary salivary canal.

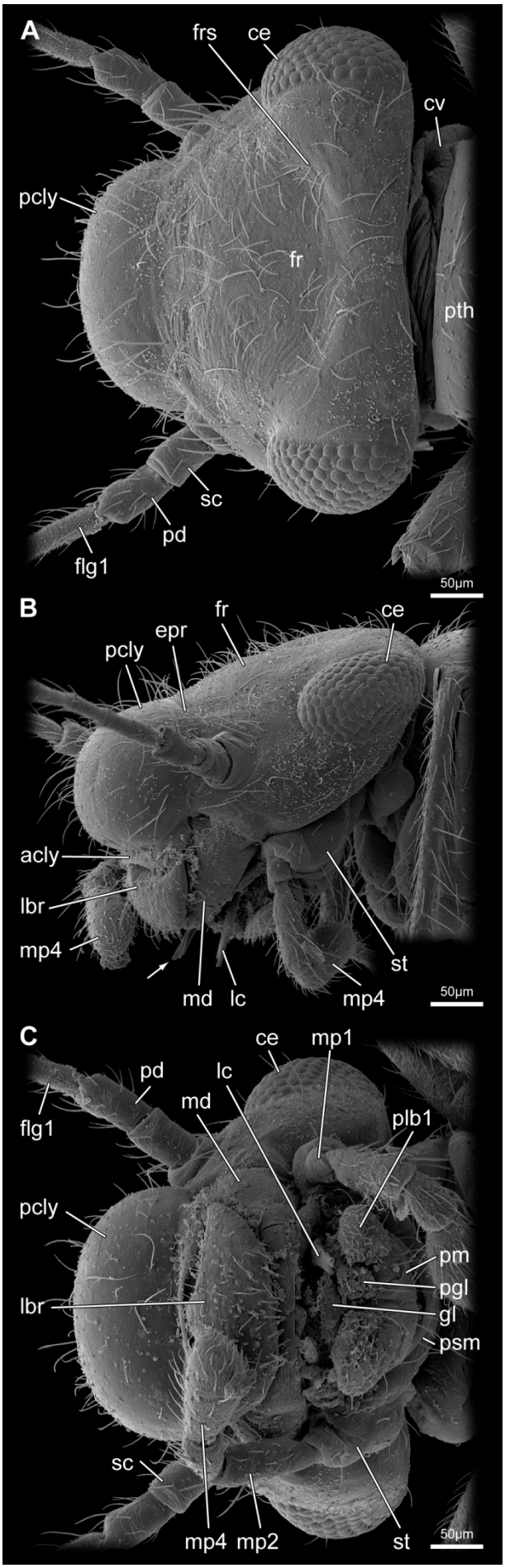
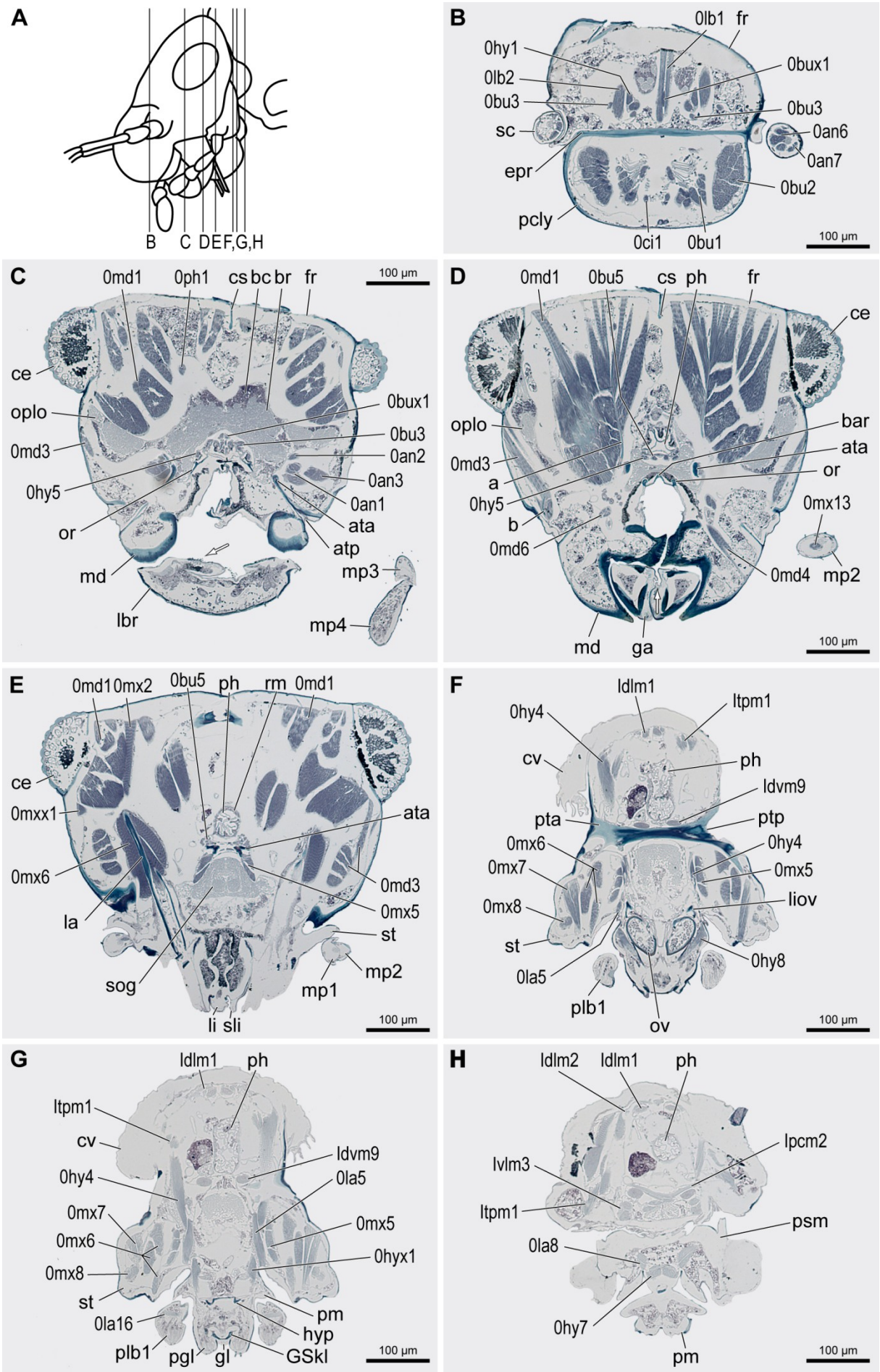


Figure 15. *Cerobasis* sp. (Trogiomorpha), unknown sex, head and thorax, Scanning Electron Micrograph. A: dorsal view; B: lateral view; C: ventral view. acly, anteclypeus; ce, compound eye; cv, cervix; epr, epistomal ridge; flg, flagellomere with appropriate number; fr, frons; frs, frontal suture; gl, glossa; lc, lacinia; lbr, labrum; md, mandible; mp, maxillary palpomere with appropriate number; pcly, postclypeus; pd, pedicellus; pgl, paraglossa; plb, labial palpomere with appropriate number; pm, prementum; psm, postmentum; pth, prothorax; sc, scapus; st, stipes.

Figure 16 (next page). *Cerobasis* sp. (Trogiomorpha), unknown sex, head and thorax, cross sections, muscular nomenclature follows Friedrich & Beutel (2008), Wipfler et al. (2011) and Table 2. A: head and thorax (legs omitted), schematic, lateral view showing planes of section of light micrographs B – H. Arrow in C indicates epipharyngeal brush. Arrow in D indicates linkage of galeae. a, adductor tendon; ata, anterior tentorial arm; atp, anterior tentorial pit; b, abductor tendon; bar, median bar located between bases of oral hypopharyngeal arms; bc, bark cell; br, brain; ce, compound eye; cs, coronal suture; cv, cervix; epr, epistomal ridge; fr, frons; ga, galea; gl, glossa; GSkl, Gabelsklerit; hyp, hypopharynx; la, lacinia; lbr, labrum; li, lingua; liov, ligament connecting sitophore with ovoid sclerite; md, mandible; mp, maxillary palpomere with appropriate number; oplo, optic lobe; or, oral arm of hypopharynx; ov, ovoid sclerite of hypopharynx; pd, pedicellus; pgl, paraglossa; ph, pharynx; plb, labial palpomere with appropriate number; pm, prementum; psm, postmentum; pta, posterior tentorial arm; pth, prothorax; ptp, posterior tentorial pit; rm, ring muscle layer of pharynx; sc, scapus; sli, superlingua; sog, subesophageal ganglion; st, stipes.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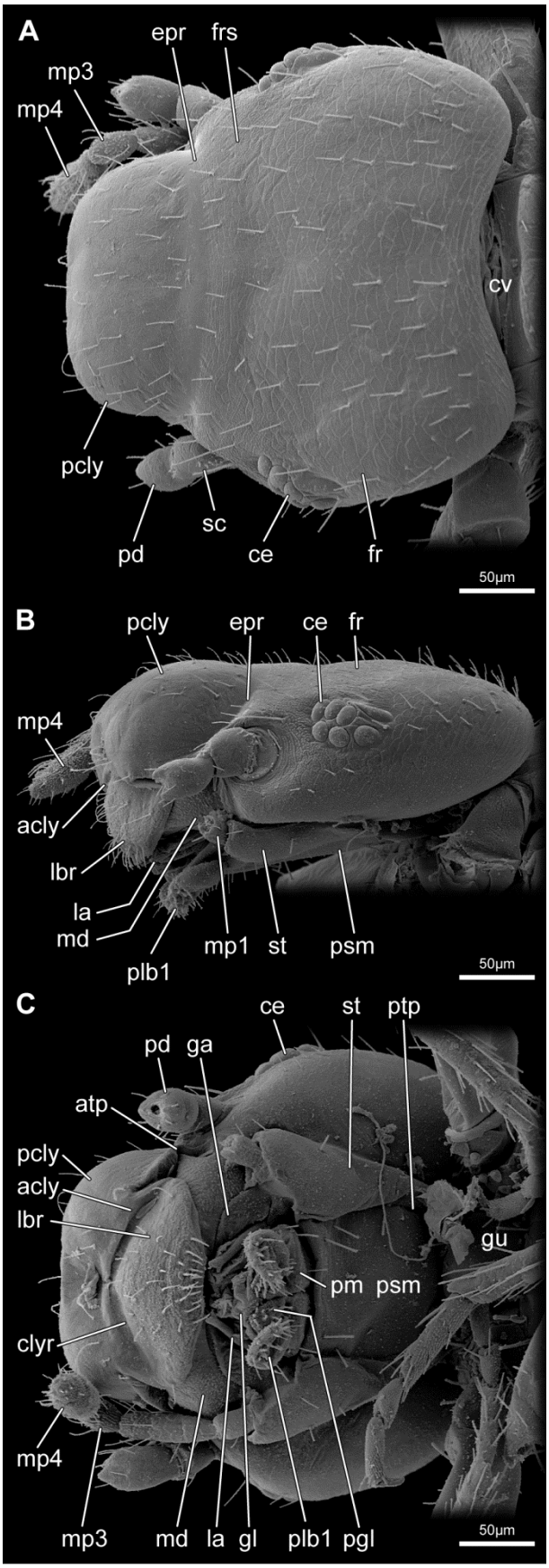
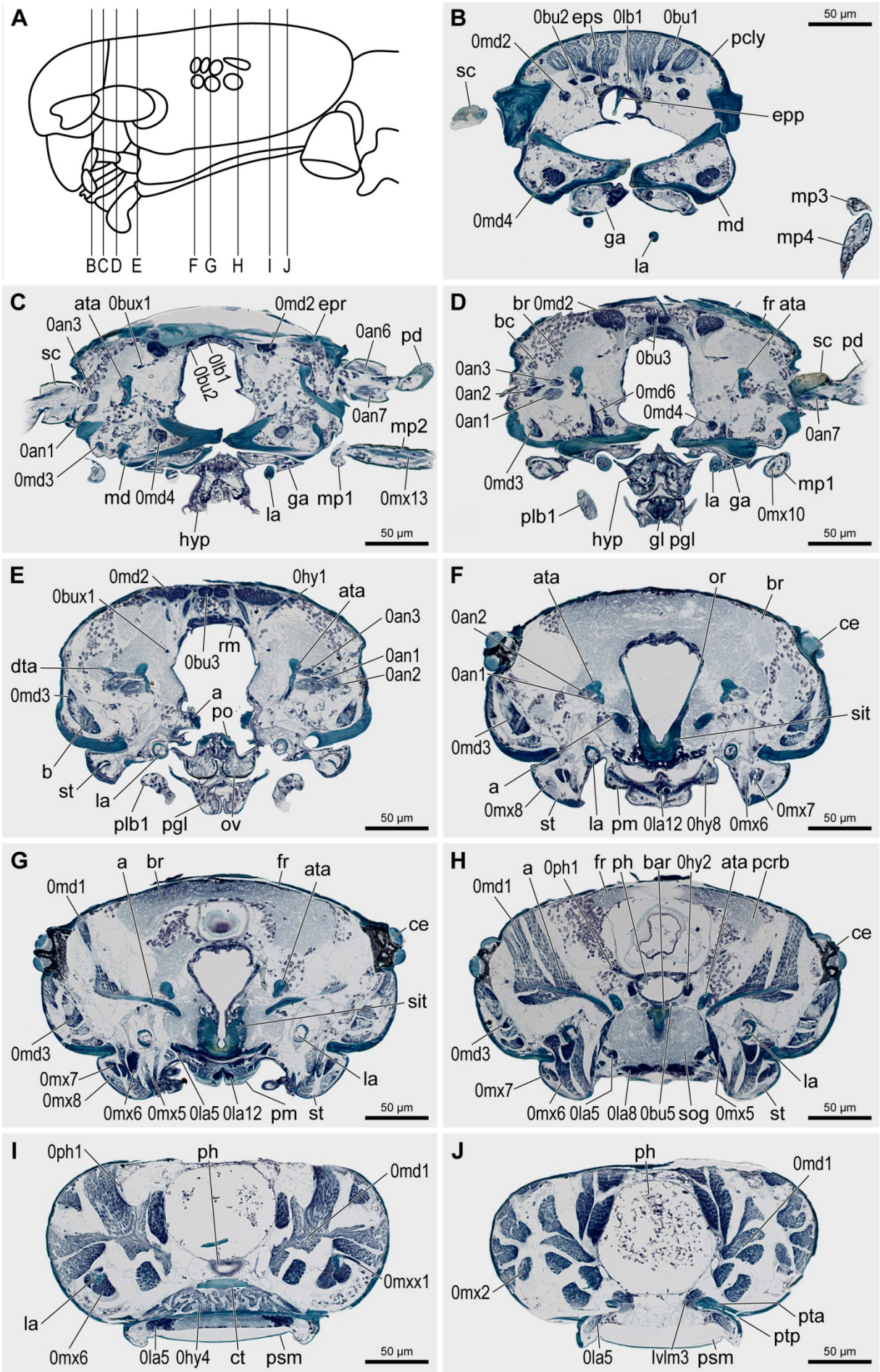


Figure 17. *Liposcelis decolor* (Troctomorpha), unknown sex, head and thorax, Scanning Electron Micrograph. Both antennae damaged with missing flagellomere, three distal segments of maxillary palp missing on the left. A: dorsal view; B: lateral view; C: ventral view. acly, anteclypeus; atp, anterior tentorial pit; ce, compound eye; clyr, clypeolabral ridge; cv, cervix; epr, epistomal ridge; fr, frons; frs, frontal suture; ga, galea; gl, glossa; gu, gula; la, lacinia; lbr, labrum; md, mandible; maxillary palpomere with appropriate number; pd, pedicellus; pgl, paraglossa; plb, labial palpomere with appropriate number; pm, prementum; psm, postmentum; ptp, posterior tentorial pit; sc, scapus; st, stipes.

Figure 18 (next page). *Liposcelis decolor* (Troctomorpha), unknown sex, head, cross sections. Muscular nomenclature follows Friedrich & Beutel (2008), Wipfler et al. (2011) and Table 2. A: head and thorax (legs omitted), schematic, lateral view showing planes of section of light micrographs B – J. a, adductor tendon; ata, anterior tentorial arm; b, abductor tendon; bar, median bar located between bases of oral hypopharyngeal arms; bc, bark cell; br, brain; ce, compound eye; ct, corpotentorium; dta, dorsal tentorial arm; epp, epipharyngeal pestle; epr, epistomal ridge; fr, frons; ga, galea; gl, glossa; hyp, hypopharynx; la, lacinia; md, mandible; mp, maxillary palpomere with appropriate number; or, oral arm of hypopharynx; ov, ovoid sclerite of hypopharynx; pcrb, protocerebrum; pd, pedicellus; pgl, paraglossa; ph, pharynx; plb, labial palpomere with appropriate number; pm, prementum; po, posterior arm of hypopharynx; psm, postmentum; pta, posterior tentorial arm; ptp, posterior tentorial pit; rm, ring muscle layer; sc, scapus; sit, sitophore of hypopharynx; sog, subesophageal ganglion; st, stipes.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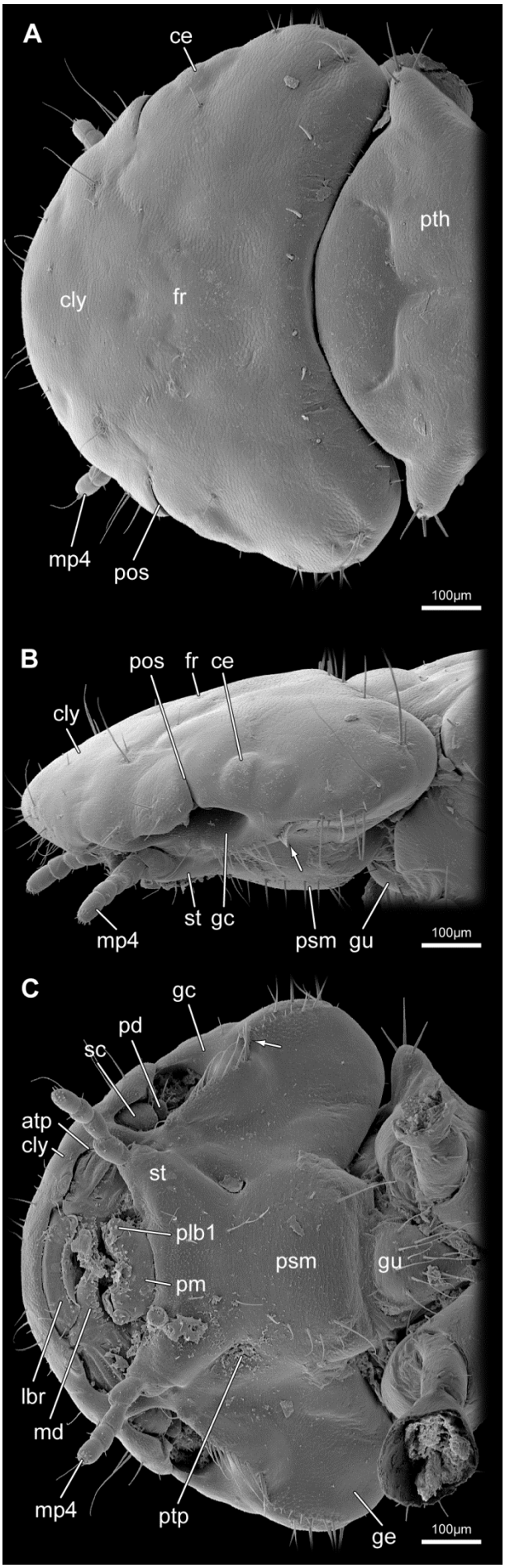


Figure 19. *Piagetiella caputincisum* (Amblycera), unknown sex, head and thorax, Scanning Electron Micrograph. Both antennae damaged, third antennomere missing. A: dorsal view; B: lateral view; C: ventral view. atp, anterior tentorial pit; ce, compound eye; cly, clypeus; fr, frons; gc, genal cavity for antenna (homologous to "ga" in Spangenberg et al. 2013a); ge, gena; gu, gula; lbr, labrum; md, mandible; mp4, fourth maxillary palpomere; pd, pedicellus; plb1, first labial palpomere; pm, prementum; pos, preocular slit; psm, postmentum; pth, prothorax; ptp, posterior tentorial pit; sc, scapus; st, stipes. Arrow indicates genal rim equipped with sensilla in a comb-like configuration.

Figure 20 (next page). *Piagetiella caputincisum* (Amblycera), unknown sex, head, cross sections, muscular nomenclature follows Friedrich & Beutel (2008), Wipfler et al. (2011) and Table 2. A: head and thorax (legs omitted), schematic, lateral view showing planes of section of light micrographs B – H. a, adductor tendon; apov, posterior apodeme of ovoid sclerite; ata, anterior tentorial arm; b, abductor tendon; br, brain; ce, compound eye; cl, corpora labialia; cly, clypeus; clyl, clypeal ligament; cpc, circumesophageal connective; ct, corpotentorium; fg, frontal ganglion; ga, galea; gc, genal cavity for antenna (homologous to "ga" in Spangenberg et al. 2013a); gl, glossa; hyp, hypopharynx; la, lacinia; liov, ligament connecting sitophore with ovoid sclerite; md, mandible; mp, maxillary palpomere with appropriate number; nct, nucleus of connective tissue; nl, neural lamella; np, neuropil; or, oral arm of hypopharynx; pd, pedicellus; pgl, paraglossa; ph, pharynx; plb1, first labial palpomere; pm, prementum; po, posterior arm of hypopharynx; pta, posterior tentorial arm; ptp; posterior tentorial pit; sal, salivarium; sc, scapus; sep, sclerotization of epipharynx, epipharyngeal sclerite; sg, salivary gland; sit, sitophore of hypopharynx; sog, subesophageal ganglion; st, stipes.

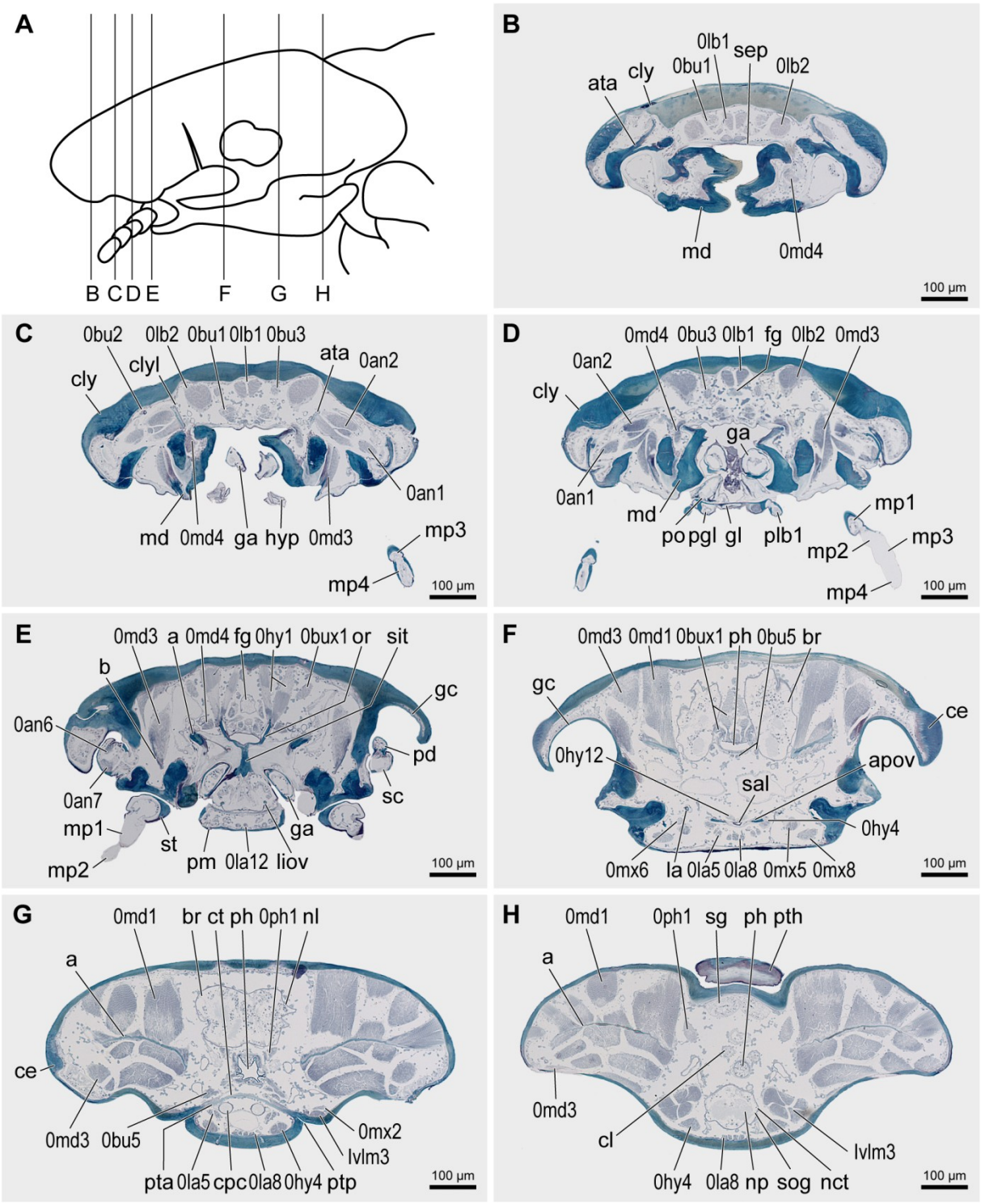
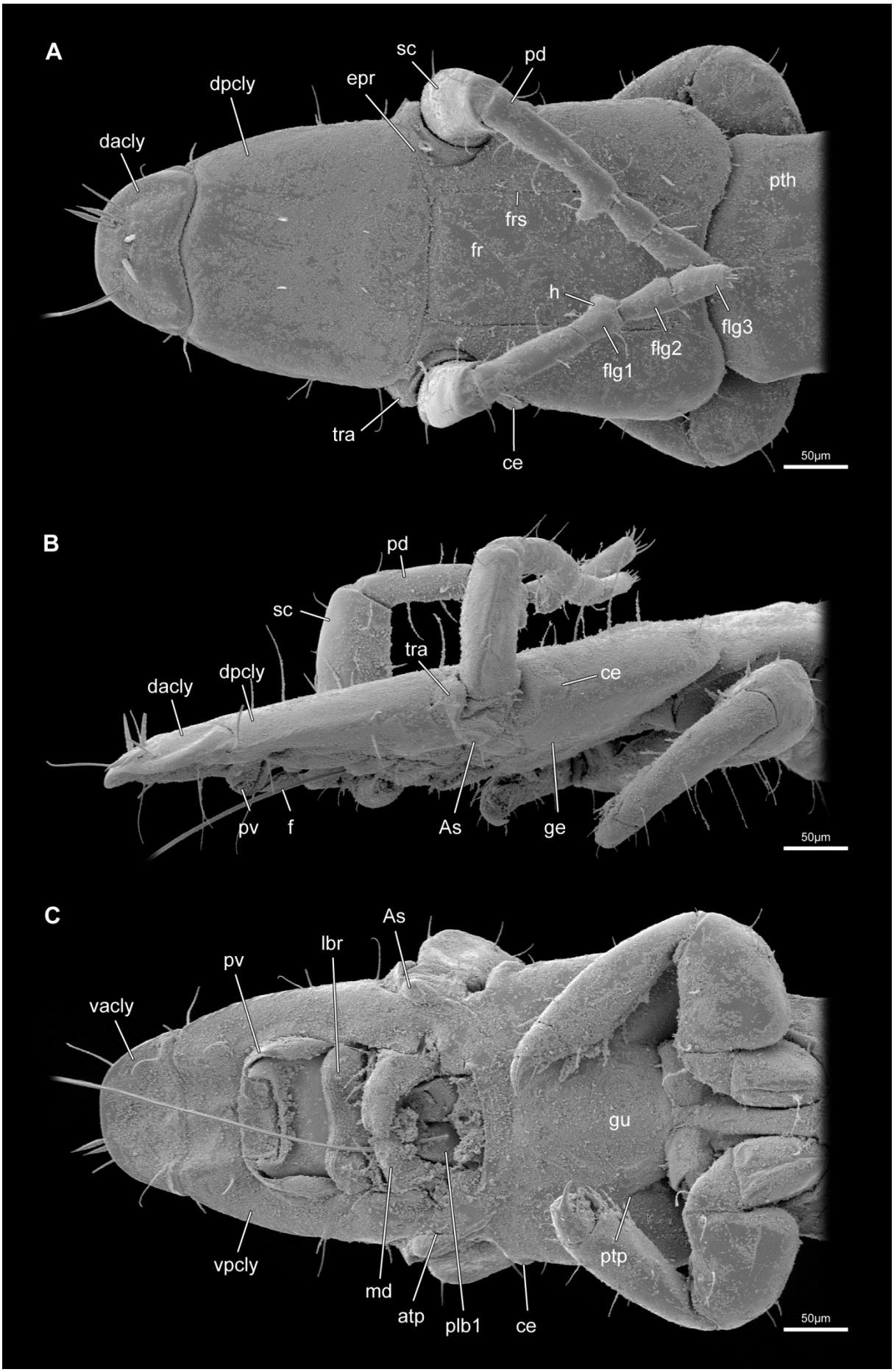


Figure 21 (next page). *Columbicola columbae* (Ischnocera), male, head and thorax, Scanning Electron Micrograph. A: dorsal view; B: lateral view; C: ventral view. As, “Antennenschuppe” of Risler (1951); atp, anterior tentorial pit; ce, compound eye; dacly, dorsal region of anteclypeus; dpcly, dorsal region of postclypeus; f, part of a bird’s feather; fr, frons; frs, frontal suture; ge, gena; gu, gula; h, hook of first antennal flagellomere; lbr, labrum; md, mandible; pd, pedicellus; plb1, first labial palpomere; pth, prothorax; ptp, posterior tentorial pit; pv, pulvinus; sc, scapus; tra, trabeculum; vacly, ventral region of anteclypeus; vpcly, ventral region of postclypeus.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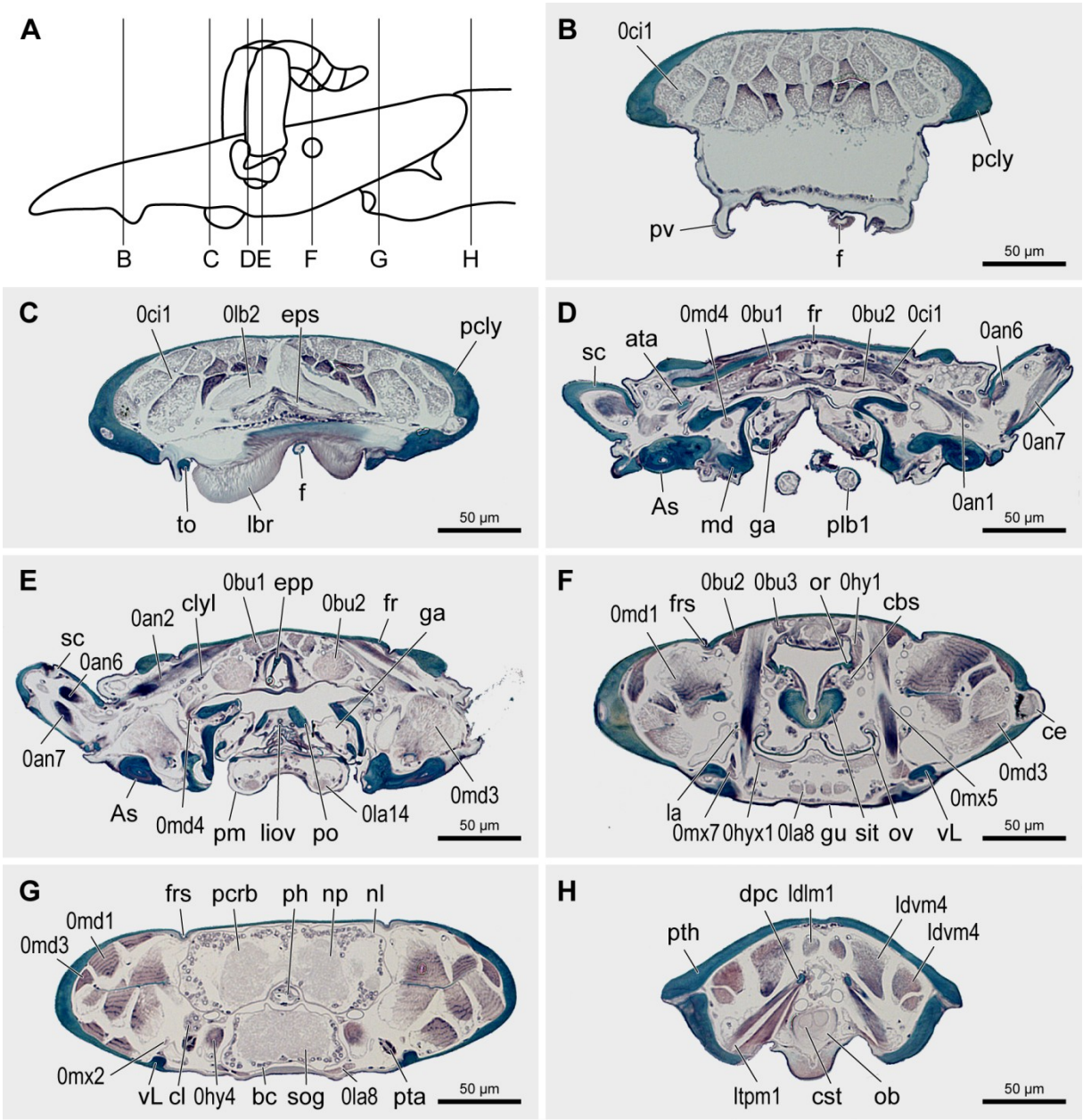
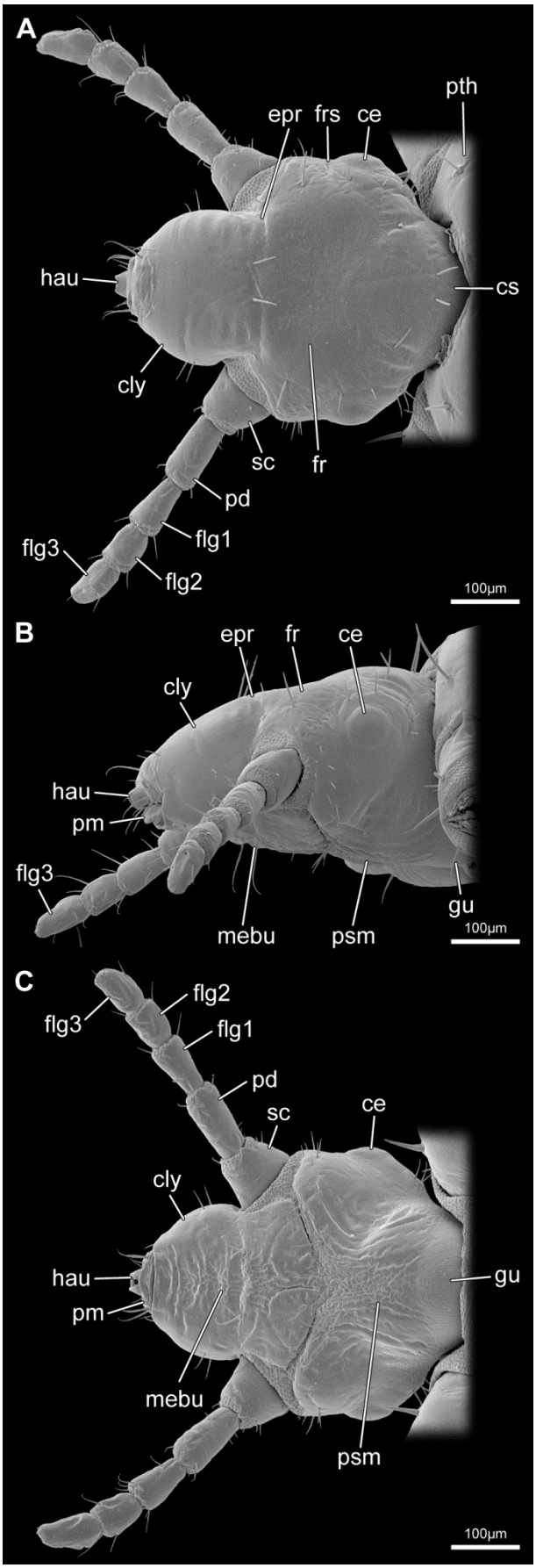


Figure 22. *Columbicola columbae* (Ischnocera), unknown sex, head and thorax, cross sections, muscular nomenclature follows Friedrich & Beutel (2008), Wipfler et al. (2011) and Table 2. A: head and thorax (legs omitted), schematic, lateral view showing planes of section of light micrographs B – H. As, “Antennenschuppe” of Risler (1951); ata, anterior arm of tentorium; bc, bark cell; cbs, cibarial sense organ; ce, compound eye; cl, corpora labialia; clyl, clypeal ligament; cst, connectives between subeosophageal ganglion and first thoracal ganglion; dpco, dorsal postoccipital condylus; epp, epipharyngeal pestle; eps, epipharyngeal sense organ; f, part of feather; fr, frons; frs, frontal suture; ga, galea; gu, gula; la, lacinia, liov, ligament connecting sitophore with ovoid sclerite (“Chitinfaden” of Haub 1972); md, mandible; nl, neural lamella; nr, neuropil; ob, obturaculum; or, oral arm of hypopharynx; ov, ovoid sclerite of hypopharynx; pcrb, protocerebrum; ph, pharynx; plb1, first labial palpomere; po, posterior arm of hypopharynx; pta, posterior tentorial arm; pth, prothorax; pv, pulvinus; sc, scapus; sit, sitophore of hypopharynx; sog, subesophageal ganglion; to, torma; vL, "ventrale Längsleisten" (Risler 1951) enclosing labium and gula.



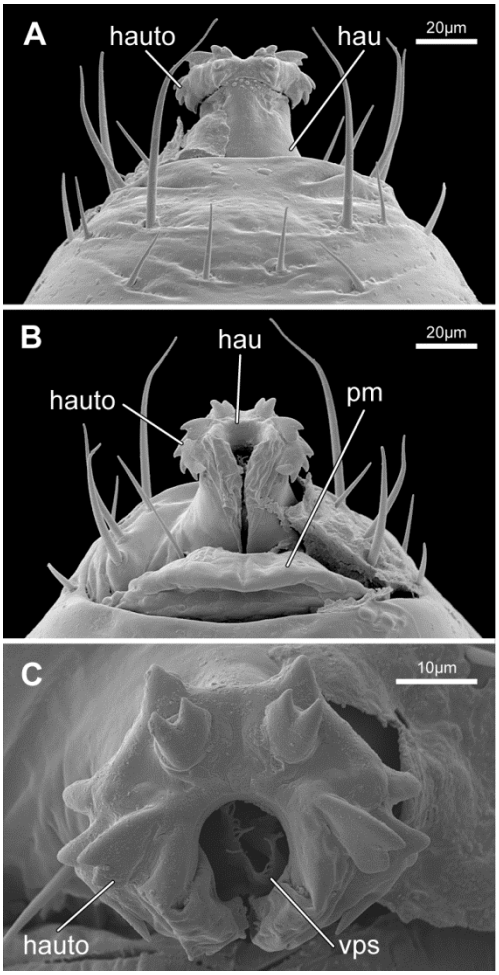
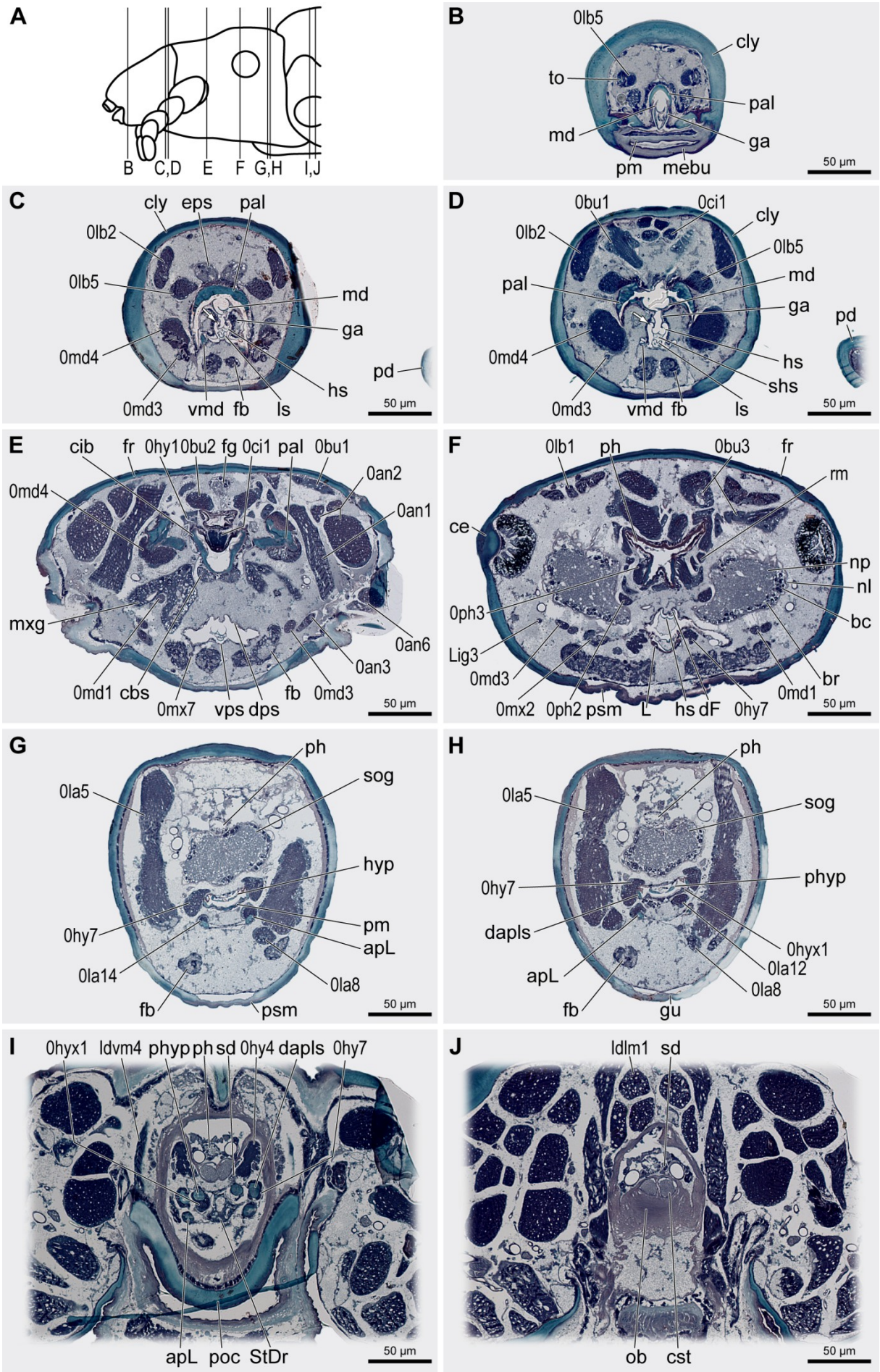


Figure 24. *Pediculus* (*humanus*) *corporis* (Anoplura), female, proboscis evaginated, left side dirty, Scanning Electron Micrograph. Another individual than in Fig. 23. A: dorsal view; B: ventral view; C: frontal view. hau, haustellum; hauto, sclerotized tooth of haustellum; pm, prementum; vps, ventral part of anopluran piercer sheath, ventral prementum.

Figure 23 (left side). *Pediculus* (*humanus*) *corporis* (Anoplura), females, head and thorax, Scanning Electron Micrograph. B is another individual than A and C. A: dorsal view, B: lateral view, C: ventral view. ce, compound eye; cly, clypeus; cs, coronal suture (see also Stojanovich 1945, fig. 11); epr, epistomal ridge; flg, flagellomere with appropriate number; fr, frons; frs, frontal suture (see also Stojanovich 1945, fig. 11); gu, gula; hau, haustellum (invaginated condition); mebu, membranous bulge ("ventromedianer Membranwulst der vorderen Kopfkapsel" Tröster 1990a); pd, pedicellus; pm, prementum; psm, postmentum; pth, prothorax; sc, scapus.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B
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apL
poc
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50 µm
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ldlm1
sd
ob
cst
50 µm

Figure 25 (previous page). *Pediculus* (*humanus*) *corporis* (Anoplura), female, head, cross sections, muscular nomenclature follows Friedrich & Beutel (2008), Wipfler et al. (2011) and Table 2. A: head and thorax (legs omitted), schematic, lateral view showing planes of section of light micrographs B – J. Arrows indicate linkage of galea with hypopharyngeal stylet. apL, apodeme of L; bc, bark cell; br, brain; cbs, cibarial sense organ; ce, compound eye; cib, cibarium; cly, clypeus; cst, connectives between subeosophageal ganglion and first thoracal ganglion; dapls, dorsal apodeme of labial stylet; dF, "dorsale Führungsrinne der Stechborsten" (Tröster 1990a); dps, dorsal part of anopluran piercer sheath, dorsal hypopharynx; eps, epipharyngeal sense organ; fb, fat body (see also fig. 4 of Ramcke 1965, and figs. 9, 24 of Hirsch 1986); frontal ganglion; fr, frons; ga, galea; gu, gula; hs, hypopharyngeal stylet, dorsal bristle of Anoplura developed from ventral hypopharynx; hyp, hypopharynx; L, sclerotized elongation of limes labialis and proximal ventral piercer sheath, part of postmentum ("sklerotisierte Lasche des proximalen Stilettsackbodens = Postmentum" Ramcke 1965); Lig3, ligament of Tröster (1990a) connecting ventral side of head capsule with dorsal head capsule, ventrad the antennal articulation; ls, labial stylet, ventral bristle of Anoplura developed from prementum; md, mandible; mebu, membranous bulge "ventromedianer Membranwulst der vorderen Kopfkapsel" (Tröster 1990a); mxg, maxillary gland; nl, neural lamella; np, neuropil; ob, obturaculum; pal, palatum; pd, pedicellus; ph, pharynx; phyp, posterior tendon-like end of hypopharynx; pm, prementum; poc, postocciput; psm, postmentum; rm, ring muscle layer of pharynx; sd, salivary duct; shs, salivary canal of hypopharyngeal stylet or median salivary stylet; sog, subesophageal ganglion; StDr, "Stacheldrüse" of von Kéler (1966) and Tröster (1990a), glandular cells on the dorsal base of the prementum; to, torma; vmd, ventral part of mandible ("Mandibelplatte" of Hirsch 1986); vps, ventral part of anopluran piercer sheath, ventral prementum.

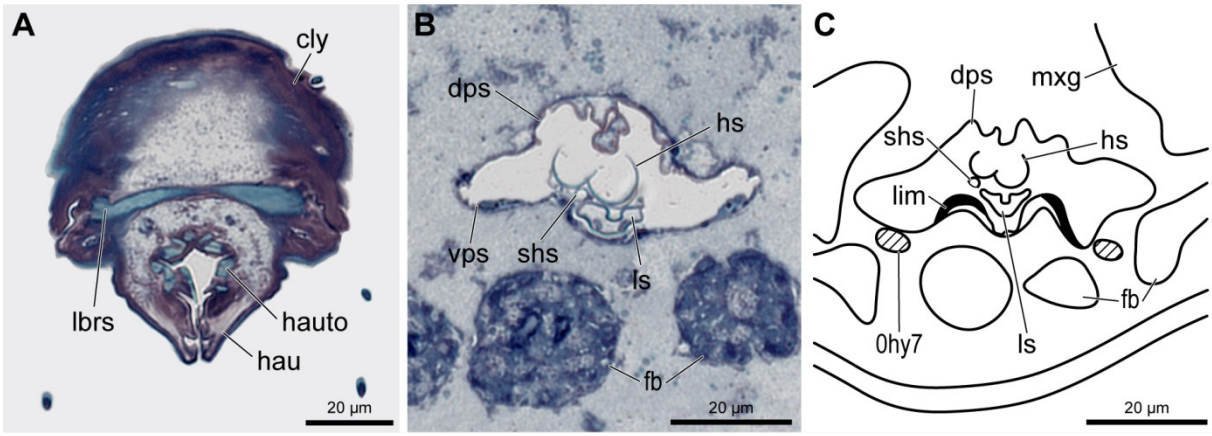

Figure 26. *Pediculus* (*humanus*) *corporis* (Anoplura), female, same individual as in Fig. 25, head, cross sections, muscular nomenclature follows Wipfler et al. (2011). A: posterior end of haustellum; B: piercer sheath, plane of section 26 µm anterad to that of Fig. 25E; C: piercer sheath schematic, plane of section 10 µm posterad to that of Fig. 25E. cly, clypeus; dps, dorsal part of anopluran piercer sheath, dorsal hypopharynx; fb, fat body; hau, haustellum; hauto, sclerotized tooth of haustellum; hs, hypopharyngeal stylet, dorsal bristle of Anoplura developed from ventral hypopharynx; lbrs, labral sclerite; lim, limes labialis; ls, labial stylet, ventral bristle of Anoplura developed from prementum; shs, salivary canal of hypopharyngeal stylet or median salivary stylet; vps, ventral part of anopluran piercer sheath, ventral prementum.

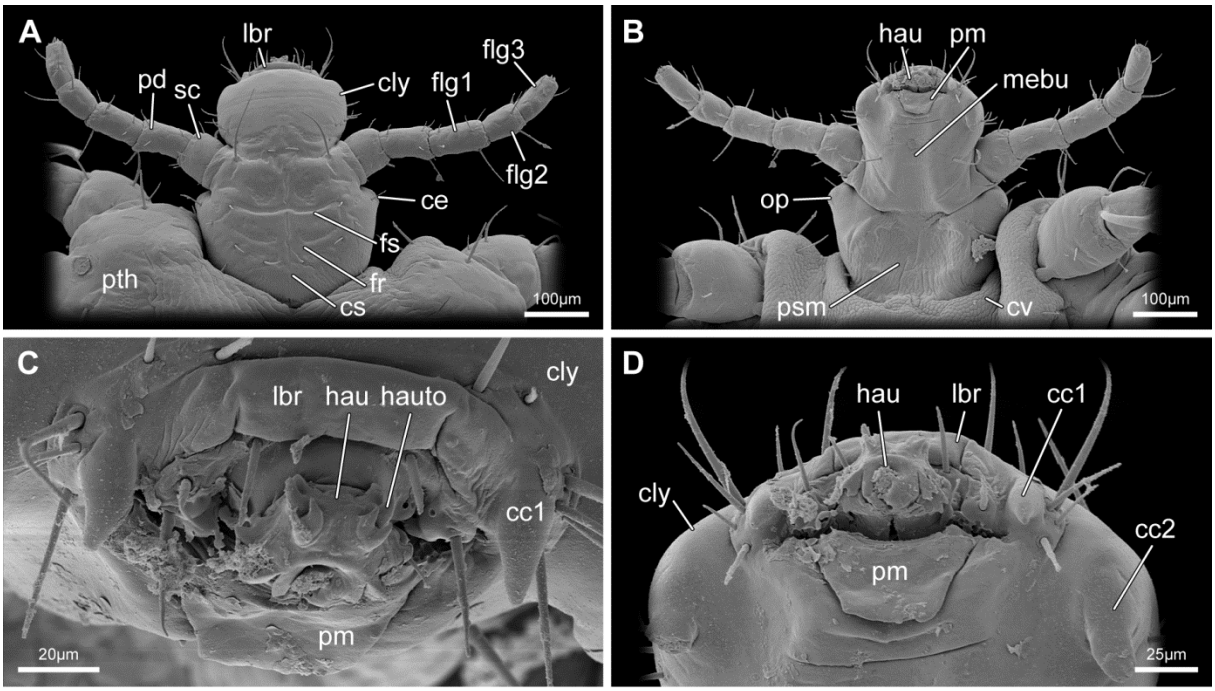

Figure 27. *Phthirus pubis* (Anoplura), female, head and thorax, Scanning Electron Micrograph. A: dorsal view; B: ventral view; C: frontal view of evaginated proboscis; D: ventral view of evaginated proboscis. cc1, first pair of clypeal cones; cc2, second pair of clypeal cones (right one damage); ce, compound eye; cly, clypeus; cs, coronal suture; cv, cervix; flg, flagellomere with appropriate number; fr, frons; frs, frontal suture; hau, haustellum; hauto, sclerotized tooth of haustellum; lbr, labrum; mebu, membranous bulge "ventromedianer Membranwulst der vorderen Kopfkapsel" (Tröster 1990a); op, ocular point; pd, pedicellus; pm, prementum; psm, postmentum; pth, prothorax; sc, scapus.

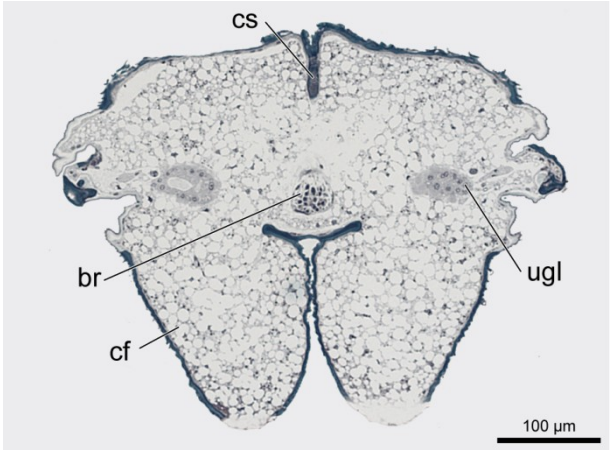

Figure 28. *Cacopsylla* sp. (Sternorrhyncha), head, cross section in the plane of the antennal base. br, brain; cf, cone-shaped protrusion of the frons; cs, coronal suture; ugl, unknown gland.

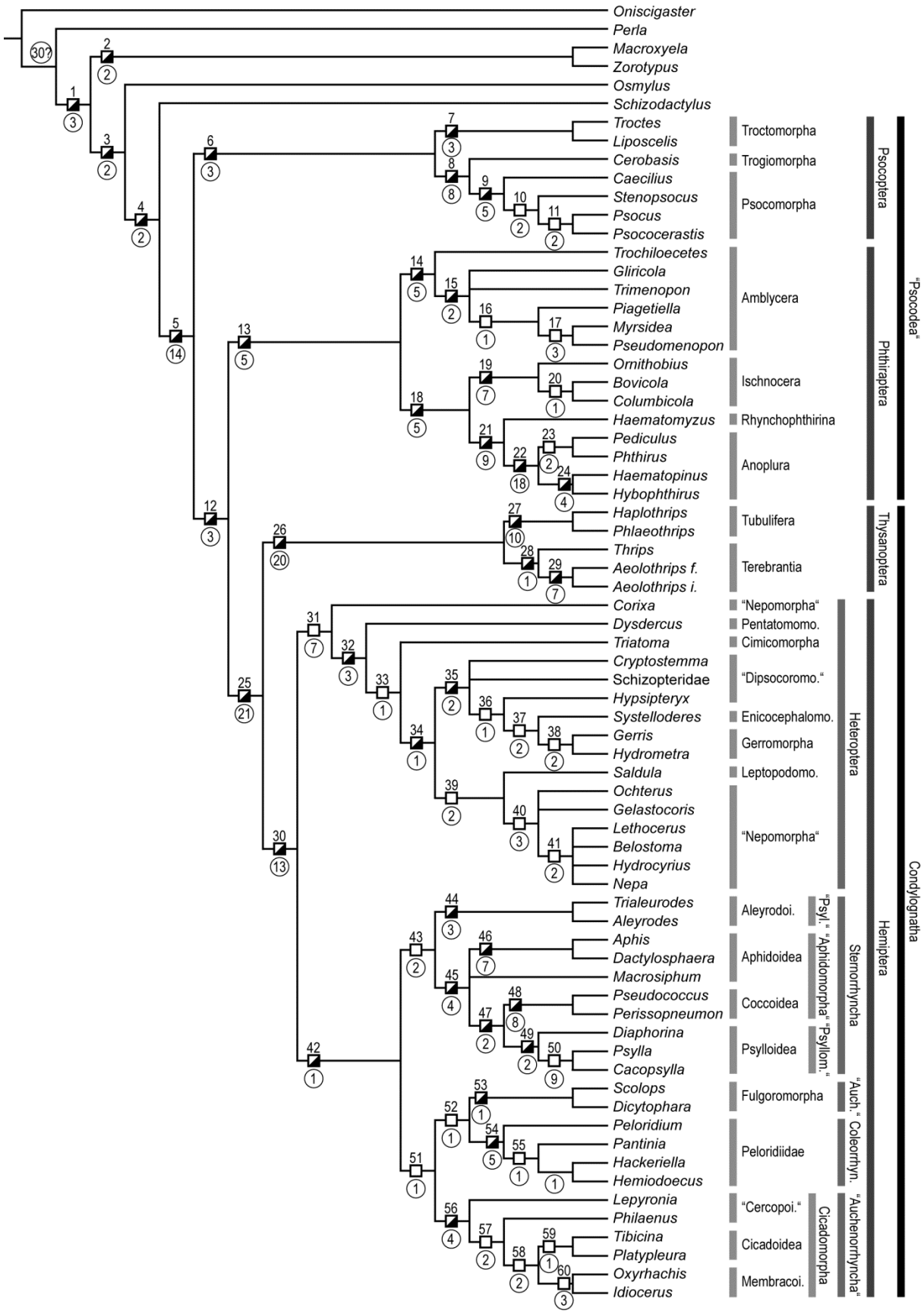
Oniscigaster
Perla
Macroxyela
Zorotypus
Osmylus
Schizodactylus
Troctes
Liposcelis
Cerobasis
Caecilius
Stenopsocus
Psocus
Psococerastis
Trochiloecetes
Gliricola
Trimenopon
Piagetiella
Myrsidea
Pseudomenopon
Ornithobius
Bovicola
Columbicola
Haematomyzus
Pediculus
Phthirus
Haematopinus
Hybophthirus
Haplothrips
Phlaeothrips
Thrips
Aeolothrips f.
Aeolothrips i.
Corixa
Dysdercus
Triatoma
Cryptostemma
Schizopteridae
Hypsipteryx
Systelloderes
Gerris
Hydrometra
Saldula
Ochterus
Gelastocoris
Lethocerus
Belostoma
Hydrocyrius
Nepa
Trialeurodes
Aleyrodes
Aphis
Dactylosphaera
Macrosiphum
Pseudococcus
Perissopneumon
Diaphorina
Psylla
Cacopsylla
Scolops
Dicytophara
Peloridium
Pantinia
Hackeriella
Hemiodoecus
Lepyronia
Philaenus
Tibicina
Platypleura
Oxyrhachis
Idiocerus
Troctomorpha
Trogiomorpha
Psocomorpha
Amblycera
Ischnocera
Rhynchophthirina
Anoplura
Tubulifera
Terebrantia
"Nepomorpha"
Pentatomomo.
Cimicomorpha
"Dipsocoromo."
Enicocephalomo.
Gerromorpha
Leptopodomo.
"Nepomorpha"
Aleyrodoi.
Aphidoidea
Coccoidea
Psylloidea
Fulgoromorpha
Peloridiidae
"Cercopoi."
Cicadoidea
Membracoi.
Psocoptera
Phthiraptera
Thysanoptera
Heteroptera
Hemiptera
"Psyl."
"Aphidomorpha"
"Psyllom."
"Auch."
Coleorrhyn.
"Auchenorrhyncha"
Sternorrhyncha
Cicadomorpha
"Psocodea"
Condylognatha

Figure 29 (previous page). Strict consensus cladogram of 397 characters (WinClada: 1352 steps, Ci: 34, Ri: 75, unambiguous only; TNT: 1342 steps) and 70 taxa (*Aleurolobus* and *Melicharia* excluded). Black-and-white boxes indicate homoplasious and non-homoplasious apomorphy-complexes, white boxes only non-homoplasious ones (not identical with those in Fig. A1; see Appendix) (apomorphies of single species not labeled). Encircled numbers indicate Bremer Support values calculated using TNT.

4. Discussion

4.1 Discussion of phylogenetic aspects

Acercaria

One central issue of acercarian phylogeny is the monophyletic origin. The present cladistic analysis of cephalic characters (including musculature, nervous system, digestive tract and salivary system) suggests that the entire lineage is indeed a clade (Bremer Support: 14), supported by nine non-homoplasious and nine homoplasious apomorphies. Characteristic apomorphies are modifications of the maxilla: the lacinia is stylet-like and detached from the stipes, the cardo (character reversal in *Aeolothrips*, *Psocus*, and partly Amblycera) and also the muscles 0mx1 (M. craniocardinalis), 0mx3 (M. tentoriocardinalis), and 0mx9 (M. stipitopalpalis medialis) are absent. The labial palp is composed of a single segment if present, and the floor of the food pump is ventrally orientated. The monophyly of Acercaria is in agreement with different morphological (e.g. Hennig 1969; Kristensen 1981, 1991; Beutel & Gorb 2001, 2006) and molecular studies (e.g. Wheeler et al. 2001; Kjer et al. 2006; Wang et al. 2013). In contrast, current molecular investigations (i.a. 1KITE: http://www.1kite.org/) based on transcriptomic data yielded paraphyletic Acercaria with Psocodea placed as sister group of Holometabola (Fig. 1C) (Misof et al. subm.; see also Ishiwata et al. 2011). This is not supported by cephalic features: Psocodea and Holometabola do not share any apomorphies of the head. Further evaluations and character state mapping are impeded by the lack of several important taxa in the 1KITE sampling (e.g. Ischnocera, Rhynchophthirina, Trogiomorpha) (Misof et al. subm.) and Ishiwata et al. (2011) (e.g. Coleorrhyncha, Fulgoromorpha, Coccoidea, Psylloidea, Troctomorpha). An alternative concept of paraphyletic Acercaria was presented by the cladistic analysis of Yoshizawa & Saigusa (2005) based on 18S rDNA (Fig. 1D). However, there is only a single potential homoplasious apomorphy supporting (Holometabola + Condylognatha) (frontal suture absent). The monophyly or paraphyly of Acercaria should be considered as an open question.

The present study shows Orthoptera is the sister group of Acercaria, and Holometabola non-monophyletic. This placement appears rather unlikely, and a clade (Acercaria + Holometabola) is widely accepted (summarized in Beutel et al. 2013b). Paraneoptera (= Acercaria + Zoraptera) (Hennig 1969) is not supported in the present study. The position of Zoraptera close to Eukinolabia (= Embioptera + Phasmatodea) is currently assumed at best (summarized in Mashimo et al. 2013).

Psocoptera

The book and bark lice are rendered monophyletic and placed as sistergroup of the remaining Acercaria in the analyses of cephalic features. The monophyly is supported by two non-homoplasious and nine homoplasious characters (BS: 3). The most conspicuous apomorphies are the presence of a collar at the base of antennal segment three and following antennomeres as tear-off device (Seeger 1975), and the tri-furcated tip of the lacinia. Other features such as for instance the presence of the mortar and pestle apparatus turned out as homoplasy, whereas Friedemann et al. (2013) showed it as apomorphy. The presence of the frontal ocellus and the two vertical ocelli is highly variable (e.g. Smithers 1972). Three ocelli are a ground plan character of Psocoptera (e.g. Jentsch 1940) and this condition is preserved in alate forms, whereas reduction is typical for wingless bark lice. This reduction in wingless forms is apparently a general trend in insect evolution (e.g. Jentsch 1940; Spangenberg et al. 2013a). In psocopterans the cardo is fused with the stipes without recognizable borders (Yoshizawa & Saigusa 2003). This condition is similar to what is found in Phthiraptera and likely an autapomorphy of Psocodea (Yoshizawa & Saigusa 2003). However, a small sclerite dorsad the stipes and separated from it by a suture was described for *Psococerastis nubila* (ENDERLEIN, 1906) (Yoshizawa & Saigusa 2003). This structure, possibly representing the cardo, was not observed in the same species by Masumoto & Nagashima (1993). Yoshizawa & Saigusa (2003) interpreted the sclerite as a secondarily detached stipital element, which is supported by the absence of tentorio-cardinal and tergo-cardinal muscles, and the subordinate placement of the species witin Psocodea.

The psocopteran mouthparts are intermediate between a generalized orthopteroid condition (biting mandibles) and the configuration of hemipterans (stylet-like laciniae detached from stipes). Two pairs of tubular glands (salivary glands) are present, paired ventral basophilous labial glands and dorsal acidophilous labial glands (e.g. Weber 1936). Some taxa (e.g. Caeciliusidae) are characterized by sexual dimorphism with larger dorsal labial glands in females than in males. Additionally, although sharing the same function, the shape of the left and right dorsal gland can differ between individuals (Weber 1936). The paired dorsal efferent labial ducts of Psocidae, Caeciliusidae and Mesopsocidae appear similar to the ducts of the accessory gland of some hemipterans (e.g. *Hackeriella*) by forming a loop anteriorly. The dorsal ducts fuse to a single duct anteriorly. The paired efferent ventral ducts are almost straight and fuse with each other anteriorly and with the common dorsal duct near the border region between the labium and hypopharynx and the salivarium (Weber 1936). The structure of the labial gland complex in Troctomorpha (“Deloderata” of Weber 1936) and Trogiomorpha (*Cerobasis*) differs from that of Psocomorpha. In Trogiomorpha both glands

are vesicular, whereas the ventral gland of Troctomorpha is bi-lobed (Weber 1936). In the latter all four efferent ducts fuse to form the salivarium (Weber 1936).

An additional potential autapomorphy of Psocomorpha (with reduction in Psocidae) is the capability to produce oral silk or fibres (Weber 1936). The components of the silk are exclusively secreted by the dorsal labial gland whereas the ventral labial gland is responsible for the production of watery saliva. The latter is secreted by the salivarium and runs along the saliva groove of the glossae ("Speichelrinne" of Weber 1936) into the oral cavity. The saliva of the dorsal labial gland solidifies immediately after leaving the salivarium. Consequently, it would block the glossal salivary groove. For this reason the thread is transported along the abducted hypopharyngeal wall and is presumably also guided by the tip of the hypopharynx and the laciniae (Weber 1936). In contrast to the gelling saliva of Hemiptera which forms a salivary sheath (see 4.3.3), the saliva of Psocomorpha is not involved in the uptake of food. The silk is produced by both sexes, adults and larvae and covers the clutch and micro-habitat (Weber 1936). Yohizawa (2002) considered the absence of the stipto-galeal muscle also as an autapomorphy of Psocomorpha, whereas an independent loss of 0mx7 (M. stipitogalealis) in Condylognatha is assumed in the present study. Cephalic features are only partially suitable to resolve infraordinal relationships within Psocomorpha. Psocotae (= *Psocus* + *Psococerastis*) is weakly supported by two homoplasious characters (BS: 2) and Caeciliusetae (= *Caecilius* + *Stenopsocus*) were rendered paraphyletic. However, the monophyly of the psocomorph groups is generally accepted (Yoshizawa 2002; Johnson & Mockford 2003; Johnson et al. 2004).

An ultrastructural autapomorphy of *Liposcelis* is likely the capacity of the pharyngeal circular muscle cells to form cytoplasm- and mitochondria-rich pouches emerging into the body lumen (Chapman GB 2003). Further potentially relevant ultrastructures are the antennal sensillae which were not included in the cladistic analysis but documented in detail by Hu et al. (2009).

The branching pattern (Troctomorpha + (Trogiomorpha + Psocomorpha)) including Liposcelididae is in agreement with the traditional concept of Psocoptera (e.g. Smithers 1972). Thus, analyses of only cephalic feature do not support the placement of Troctomorpha close to Amblycera (e.g. Johnson et al. 2004; Yoshizawa & Johnson 2005, 2010) or the entire Phthiraptera (e.g. Johnson & Clayton 2003; Friedemann et al. 2013). The latter option is presently best supported (e.g. Friedemann et al. 2013), for instance by the association of *Liposcelis* with nests of birds, plumage or hairs (summarized in Grimaldi & Engel 2005).

In contrast to all published phylogenetic hypothesis (see Fig. 1) is the position of Psocoptera at the base of Acercaria and its separation from Phthiraptera. Enforcing Psocodea (as seen in Fig. A2, BS: 4) as a clade yielded the following potential apomorphies:

ocelli absent; *epistomal ridge present*; collar at the base of antennal segment three and beyond in adults as potential tear-off device (rupture-facilitating cuticle) (Seeger 1975) present; *0an3, M. tentorioscapalis lateralis present*; *0md4, M. hypopharyngomandibularis present*; tip of the lacinia tri-furcated; cardo fused with the stipes; swollen paired ovoid sclerites present; paired filamentous ligaments connecting the sitophore with the ovoid sclerite present; water vapor uptaking faculty present; *mortar and pestle apparatus present*; epipharyngeal sclerite present; *precibarium absent*; *0bu5, M. tentoriobuccalis anterior present*.

Condylognatha + Phthiraptera

The unorthodox grouping Acercaria excl. Psocoptera (BS: 3) is suggested by three non-homplasious apomorphies (insertion of 0md4, M. hypopharyngomandibularis restricted to posterior outer edge of mandibular cavity; 0mx12, M. palpopalpalis maxillae primus absent; contraction of labium during initialization of feeding) and four homoplasious apomorphic features. Considering that the clade Psocodea is supported by different sources of evidence (e.g. Trautwein et al. 2012) it appears likely that this result is an artifact (see above and Fig. A2).

Phthiraptera

The clade Phthiraptera (BS: 5) and the monophyly of its subgroups are unambiguously confirmed. The traditional branching pattern (Amblycera + (Ischnocera + (Rhynchophthirina + Anoplura))) as suggested by Lyal (1985), Kristensen (1991), Wheeler et al. (2001), Johnson & Whiting (2002), and Friedemann et al. (2013) is supported by ten apomorphies (one non-homoplasious). As in Psocomorpha the cephalic characters are apparently not suitable to resolve infraordinal relationships. The ischnoceran family Philopteridae (*Ornithobius* + *Columbicola*) emerged as paraphyletic, a result which is congruent with the molecular study of Johnson & Whiting (2002). Smith (2001) even suggested that “they are almost certainly para- or polyphyletic with respect to other ischnoceran lice and are generally regarded as miscellaneous collection of genera defined by their exclusion from other ischnoceran higher taxa”.

The internal amblyceran relationships are incompletely resolved. Menoponidae is monophyletic (see also Clay 1970) and Ricinidae is the sister group of the three families Gyropidae, Trimenoponidae, and Menoponidae. The position of Ricinidae is compatible with the results of previous molecular studies (Johnson & Whiting 2002; Barker et al. 2003), whereas the latter studies showed Menoponidae is not monophyletic (see also Yoshizawa & Johnson 2003) but “this relationship had low support” (Barker et al. 2003).

The topology of Anoplura is highly incongruent between studies based on morphological (including chaetotaxy and genitalia) and molecular data, respectively. Kim & Ludwig (1978) placed (Pediculidae + Haematopinidae) as sister group to (Hybophthiridae + Phthiridae). A hypothesis also supported here appears more likely, a pattern (Pediculidae + Phthiridae) + (Haematopinidae + Hybophthiridae) (Barker et al. 2003; Light & Reed 2009; Light et al. 2010).

Cephalic evidence for polyphyletic Phthiraptera with a placement of Amblycera as sister group to Liposcelididae (predominately based on molecular data, e.g. Johnson et al. 2004; Yoshizawa & Johnson 2005, 2006, 2010) is absent. A group (Anoplura + Amblycera) as a preliminary result of 1KITE (Misof et al. subm.) appears also unlikely under morphological considerations.

Condylognatha

The evidence of a sister group relationship (Thysanoptera + Hemiptera) as rendered by cephalic characters is very strong (BS: 21; 27 apomorphies with 13 non-homoplasies). The most conspicuous features are the stylet-like mandible(s) for piercing situated in a gnathal pouch, and the laciniae locked to form at least one canal and equipped with a sclerotized maxillary lever. These characters in combination with the basin-shaped salivary pump and the sclerotized piston are essential for supply and uptake of liquid foods. A fundamentally different way of ingestion liquids has evolved independently in Anoplura, Rhynchophthirina and *Trochiloecetes* (Ischnocera) (Haub 1983) (see below). The present study contributes to the acceptance of Condylognatha which was also recently confirmed by 1KITE (Misof et al. subm.). In contrast, only two apomorphies (presence of an “Ocellushügel”; presence of 0hyx1, “M. protractor hypopharyngis”) characterize a potential clade Micracercaria (e.g. Jamieson 1987; Wheeler et al. 2001; Willmann 2005).

The sister group relationship (Thysanoptera + Hemiptera) is also tentatively supported by a similar ontogenetic development of the gnathal appendages, verified in *Haplothrips* (Thysanoptera), *Macrosteles* (Auchenorrhycnha) and *Oncopeltus* (Heteroptera) (Newcomer 1948; Heming 1980; Leggett 1985). According to Heming (1980) the common ancestor of the hemipteroid assemblage is characterized by “small, paired mandibles, short lacinial stylets, a weakly developed cibarial pump, and prominent maxillary and labial palpi”. The loss of the right mandible of Thysanoptera occurred after the split in the hemipteran and thysanopteran lineage (Heming 1980). In contrast to Thysanoptera the anlagen of the maxillary palps and labial palps are absent in the development of Hemiptera (Muir & Kershaw 1912; Newcomer 1948; Singh 1971).

Thysanoptera

The monophyly of thrips is very well supported (BS: 20; 20 apomorphies including ten non-homoplasies), fully compatible with previous results of morphological (summarized in Moritz 2006) and molecular studies (e.g. Crespi et al. 1996; Mound & Morris 2007), and also confirmed by transcriptome analyses (Misof et al. subm.). The monophyly of the subgroups Terebrantia (BS: 1) and Tubulifera (BS: 10) is also supported and consistent with Moritz (2006).

The structure of the tentorium is highly variable within Thysanoptera. In the presumably basal Aeolothripidae (Terebrantia) it is composed of the anterior arms, the posterior arms and the corpotentorium. In Melanthripinae (Aeolothripidae) stout dorsal tentorial arms are present whereas posterior arms ("Apodem") are missing. In the vast majority of Thysanoptera only bean-shaped (Terebrantia: Heterothripidae, Panchaetothripinae [Thripidae]; Tubulifera: Phlaeothripidae) or Y-shaped (Thripinae, Thripidae, Terebrantia) vestiges of the tentorium are maintained (summarized in Moritz 1982a; 2006). The branches of the Y-shaped rudiment are likely formed by the anterior and dorsal arms. It is likely that partial reduction took place independently in Thysanoptera, Heteroptera, Anoplura and Rhynchophthirina.

As already described for Coleorrhyncha (Spangenberg et al. 2013a) the presence of macropterous wings and thus the capability to fly is apparently linked with the presence of ocelli (Mound 1995).

The most unusual autapomorphy of Thysanoptera is the far-reaching reduction of the right mandible in adults. Both mandibular anlagen are present in the early embryogenesis but the right degenerates during katatrepsis (Heming 1978, 1980). Heming (1980) suggested this as an example of phylogenetic degeneration of a vestigial organ. The "Tragarm des Pharynx" (Peterson 1915) as sclerotized ridge partly connecting the labrum with the hypopharynx with the mandibular base is similar in position to the mandibular stylet and predominately discussed as rudiment of the right mandible (Peterson 1915; Risler 1957). Mickoleit (1963) supported this homology by the innervation of M. retractor mandibulae by the N. mandibularis and its insertion on the Tragarm. The alternative concepts based on embryological data favors the affiliation of the Tragarm either to the labrum (Rejne 1927) or to the labrum and stipes (Gouin 1968; Moritz 1982b), and consequently the absence of the right mandibular stylet. Moritz (1982b) interpreted the remnant of the right mandibular stylet neither as rudiment nor as an effect of a population bottleneck, but as a functional evolutionary development adapted to the specialized punching and sucking feeding. The single left mandible lacks a lever-like structure (Risler 1957; Mickoleit 1963). Heming (1978) pointed out that a part of the mandibular base of *Haplothrips verbasci* (OSBORN, 1897) (Phlaeothripidae,

Tubulifera) has a different morphological origin and is hence likely homologous to the mandibular lever of Heteroptera. However, in the latter the mandibular protractor muscles inserts on the lever whereas they are apparently absent in Thysanoptera or shifted to the mandibular pouch.

Thysanoptera apparently lack a true mandibular protractor muscle (Risler 1957; Mickoleit 1961, 1963; Matsuda 1965) (see also 4.3.2). However, Risler (1957) discussed the M. clypeolabralis lateralis as potential protractor muscle as it inserts on the mandibular pouch close to the mandibular base. His finding was restricted by the previously unknown innervation. Mickoleit (1963) figured out that the potential mandibular protractor M. clypeo-labralis lateralis is innervated by frontal nerves, and thus a labral muscle in the stricter sense. However, this muscle apparently acts as a brake of the mandible during piercing (Mickoleit 1963). In contrast, Moritz (1982b) argued that the forces acting on the mandible during feeding would it push away from its original position in the case of a pure brake, and that the muscle consequently acts as a real mandibular protractor. The view of Moritz (1982b) is supported by data of larvae where the M. clypeo-labralis lateralis is described also as mandibular protractor (Heming 1978). Heming (1980) outlined the condition of the mandibular musculature in the thysanopteran progenitor similar to that of Psocoptera. During evolution the mandible adapted to piercing which is accompanied by the loss of the primarily articulation with the head. The new spatial orientation allows more protraction and retraction than adduction and abduction. In this context, Heming (1980) stated that “the left mandibular adductors were unable to make the transition from an adductor to a protractor role and were lost.” One can speculate if these evolutionary constrains are also applicable for the protraction of the hemipteran mandibular stylet, as the mandibular protractors (0mdx4, M13, M. protractor setae mandibularis primus; 0mdx3, M14, M. protractor setae mandibularis secundus) insert not directly on the mandible as supposed in the acercarian ancestor, but on the mandibular lever (except Psylloidea with apparently secondarily reduction of the lever). Both Newcomer (1948) and Heming (1980) show that the mandibular lever ontogentically speaking is no primarily mandibular structure.

The maxilla of Thysanoptera is composed of the cardo (reduced in Tubulifera and partly in Terebrantia), the lacinia (maxillary stylet) which is equipped with the “Artikulationshebel”, the stipes, and the segmented maxillary palp. The galea is absent (Risler 1957; Mickoleit 1963). Reyne (1927) interpreted the “Artikulationshebel” as fusion of partly the stipes, lacinia and cardo. Its shape, position and function as muscle attachment site for indirect movement of the lacinia suggests its homology to the maxillary lever of Hemiptera (see also “maxillary lever” of Heming 1978). Assuming this homology, the M. protractor laciniae of Thysanoptera is likely homologous to the M. protractor setae maxillaries (0mxx5) of Hemiptera, thus theirs muscular origins also implies the homology of the maxillary

plate with the stipes following the appendicular concept of Evans (1973). The studies of Heming (1978, 1980) concerning the larval development of the plates laterad to the maxillary base also showed their stipital origin. Heming (1978) documented at least for *Haplothrips verbasci* a pre-apical socket of the left lacinia in which the apex of the right lacinia rests. This structure is apparently absent in other groups of Thysanoptera (Mound 1971). The lora are absent in Thysanoptera (Heming 1978). Maxillary glands are also absent (Risler 1957; Mickoleit 1963). However, Heming (1978) documented a "thick, glandular epithelium" on the lateral wall of the maxillary pouch. Although its function was not figured out, Heming (1978) speculated it likely secrets lubricants into the sac which houses the laciniae. A peculiar character of *Frankliniella* is the key-lock-like linkage of the lateroventral region of the epipharynx ("key") with the groove of the laciniae ("lock") (fig. 4 in Hunter & Ullman 1994). One can speculate the same condition in *Aeolothrips* referring to fig. 25 of Moritz (1982b), thus assuming this linkage as an apomorphic character for Thysanoptera or at least for Terebrantia.

The most comprehensive ultramicroscopic study concerning features of the thysanopteran head is available for *Frankliniella occidentalis* PERGANDE, 1895 (Thripidae, Terebrantia) (Hunter & Ullmann 1989, 1992, 1994). The paraglossa as the most distal region of the labium is equipped with ten sensilla of three different types, i.a. sensilla trichoidea, mechano-chemosensitive sensilla basiconica with cuticular collar and uni-porous, mechano-chemosensitive, and mechanosensitive sensilla basiconica without cuticular collars (Hunter & Ullman 1992). The left mandibular stylet of *Frankliniella* is perforated by three dendritic canals. The central canal contains three dendrites, while the two lateral ones located opposite to each other house each only a single dendrite. The lateral stylet canals are just developed in the proximal region of the mandible (Hunter & Ullmann 1992, 1994). Four dendritic canals containing each a single dendrite are present in the maxillary laciniae (Hunter & Ullman 1992, 1994). This is in contrast to the documentation listed in the character state matrix for Thysanoptera. In general, the sensory equipment of the feeding stylets of Thysanoptera (i.a. *Frankliniella*, but likely overlooked in other thrips, see character state matrix) resembles that of Auchenorrhyncha and Coleorrhyncha (Cobben 1978; Backus 1985; Brozek 2007). However, in the former group the stylets are perforated by more dendritic canals and dendrites. Both mandible and maxillae of *Frankliniella* are apparently devoid of scales or tooth (fig. 23 of Hunter & Ullman 1992).

Hunter & Ullman (1994) documented for *Frankliniella* also four precibarial sensilla situated on the epipharynx, and 20 cibarial sensilla situated both and epipharynx and hypopharynx. They proposed the homology to the gustatory chemosensilla of Hemiptera (see below). However, in the case of *Macrosteles* (Cicadellidae, Cicadomorpha) for instance the total of all these sensilla is located on the precibarium (fig. 3 in Backus & McLean 1982), whereas Hunter & Ullman (1994) distinguished between precibarial and cibarial arrange-

ment. Consequently, they homologized the four precibarial sensilla with the D-sensilla (see Backus & McLean 1982), the 18 proximal dorsal cibarial sensilla with the P-sensilla, and the other two proximal ventral cibarial sensilla with the H-sensilla. The homology is additionally supported by the position of the precibarial valve separating the sensilla in a distal (D-sensilla) and proximal (P-, H-sensilla) field (Hunter & Ullman 1996). As in Hemiptera the precibarial valve is equipped with a muscle, apparently M. labro-epipharyngealis, and acts as regulator of the food uptake in combination with the precibarial and cibarial sensilla distinguishing plant saps (Hunter & Ullman 1996).

Hemiptera

The monophyly of Hemiptera is undisputed (BS: 13; 25 apomorphies including ten non-homoplasies; Kjer 2004; Yoshizawa & Johnson 2005; Grimaldi & Engel 2005; Misof et al. subm.). The main characteristics are the presence of mandibular plates (lora), the symmetry of the mandibles encircling the laciniae, barb-like structures at the mandibular tip, the presence of a mandibular lever, the labial tube-like sheath for the mandibles and lacinae, the formation of the salivary pumping chamber by the hypopharynx, and the opening of the salivarium or pumping chamber between the maxillary stylets. In contrast to the strongly supported monophyly, the branching pattern within Hemiptera is presently far from being settled.

The mandibular stylets of phytophagous taxa are flexible to enable a curved piercing canal in the host tissue, and are characterized by a curved tip acting as an anchor and guiding device for the maxillae. In contrast, the mandibles of carnivorous Heteroptera are straight and stout (summarized in Miles 1968). Serrate tips with different extensions and number of dentations are presumably a ground plan character of Hemiptera and additionally documented for Cicadellidae (Tavella & Arzone 1993; Leopold et al. 2003; Wiesenborn 2004; Zhao et al. 2010), Psyllidae (Ullman & McLean 1986), Delphacidae (Mora et al. 2001), Pyrrhocoridae (Rani & Madhavendra 1995), and Pentatomidae (Rani & Madhavendra 1995). The hypothesis “more mandibular teeth in carnivorous Heteroptera than in phytophagous members” is supported by Faucheux (1975) and Cohen (1990). Furthermore, the barbs of carnivorous heteropterans are directed proximally whereas those of phytophagous species point distally (summarized in Boyd et al. 2002). The presence of mandibular barbs is also linked with the capability of forming salivary sheaths. Thus, the barbs are distinct in the case of anchoring in the host tissue in non-sheath forming species, and small in species applying a salivary sheath acting as guiding device (summarized in Boyd et al. 2002).

The linkage of the maxillae to form a food canal and a salivary canal is apparently a ground plan character of Hemiptera. Both canals get fused and form a common duct at the

outermost maxillary tips at least in Auchenorrhyncha (Backus 1985), Aphididae (Uzest et al. 2010) and Psyllidae (Garzo et al. 2012). The common maxillary duct of Aphididae for instance measures a mean length of 4,3 µm in relation to a mean total length of the feeding stylets of 513,3 µm (Uzest et al. 2010). The presence of a common duct apparently requires a valve mechanism for the discharge of ingested liquids into the food canal instead of the salivary canal. Neither Backus (1985) nor Uzest et al. (2010) nor Garzo et al. (2012) documented such structure. Smooth maxillary tips additionally to those species listed in the character matrix are at least present in Cicadellidae (Tavella & Arzone 1993; Leopold et al. 2003; Zhao et al. 2010), Delphacidae (Mora et al. 2001), Pyrrhocoridae (Rani & Madhavendra 1995), and Pentatomidae (Rani & Madhavendra 1995). The salivary canal at least in Cicadellidae is predominately formed by the right maxillary stylet while the left is only for delimitation (Tavella & Arzone 1993). Leopold et al. (2003) gave the theory that the surface structure of the maxillary stylets is linked with the formation of salivary sheaths. Thus, a completely smooth surface is characteristic for sheath-producing groups whereas the maxillae of lacerate and flush feeding (including predaceous) members are equipped with serrations. So far, this theory can be confirmed for Cicadellidae and Delphacidae (see above). The external opening of the maxillary food canal is referred as “functional mouth”. Cobben (1978) distinguished also between serrated tips in carnivorous Heteroptera and non-serrated in phytophagous members.

The feeding stylets are equipped with sensory structures, i.a. stylet or dendritic canals with one or numerous dendrites supplying one or numerous stylet sensilla (see Backus 1985). Sensilla associated with the stylets are detectable at best with Transmission Electron Microscopy. Chapman (1982) recorded up to five pairs of sensilla in the maxillary and mandibular stylets in the ground plan of Hemiptera. However, Backus & McLean (1982) documented three mechnanoreceptive sensilla in each of the fourth stylets of a cicadellid species. According to Backus (1988) these proprioceptive and mechanoreceptive sensilla detect the position of the stylets in the host tissue and are primarily restricted to phytophagous members. Cobben (1978) and Backus (1988) reported sensilla innervations and appropriate canals both for mandibles and maxillae in Thysanoptera, Cimicomorpha (see also Cohen 1990), Gerromorpha and Auchenorrhyncha, and a single innervation or canal only of the mandibular stylet for Sternorrhyncha and Pentatomomorpha (see also Peregrine 1972b). The single-canal mandibles of the cicadomorph *Macrosteles* (Cicadellidae, Membracoidea) are innervated each by three dendrites, and the maxillae each by two dendrites in the canal situated near the salivary canal and three in the canal close to food canal (Forbes & Raine 1973; Backus & McLean 1982; Backus 1985). The three sensilla of each mandibular stylet are innervated each by a single dendrite. In contrast, the three sensilla of the maxillary stylet are innervated each by two dendrites (Backus 1985). Two maxillary dendritic canals and one

mandibular dendritic canal were also documented for Cicadellidae (Leopold et al. 2003; Zhao et al. 2010). It has to be taken in account, that the maxillary canal at least of Auchenorrhyncha is unpaired at its base and just splits into two canals distally (Backus 1985; compare figs. 21 and 23 in Leopold et al. 2003). The stylet sensory system of Fulgoromorpha is more complex. The single-canaled mandible of *Nilaparvata lugens* (Stål, 1854) (Delphacidae) is equipped each with five dendrites (e.g. Foster et al. 1983b). The innervation of the two-canaled maxillae is identical to that described in Cicadomorpha (Backus 1985). The five sensilla per maxillary stylet are innervated each by a single dendrite. In contrast, the three mandibular sensilla are innervated each by two dendrites which is the opposite condition in comparison to *Macrosteles* (Backus 1985). Forbes (1977) reported for the sternorrhynchous Aphididae a single mandibular duct containing two dendrites. The appropriate maxillae are devoid of canals. The maxillary and mandibular stylets of *Sinea confusa* CAUDELL, 1901 (Reduviidae, Cimicomorpha) are each perforated by a single dendritic canal (Cohen 1990). In this heteropteran there are two dendrites in the mandibular canal, and five in the maxillary canal (Cohen 1990). However, Cobben (1978) listed also reduviid species with different numbers of stylet dendrites. He reported three mandibular dendrites and five maxillary dendrites for *Pirates hybridus* (SCOPLI, 1763), and five and three, respectively, for both *Rhodnius* and *Triatoma*. Such a variable number of dendrites is also documented for further members of Cimicomorpha, Pentatomomorpha, Gerromorpha, and Nepomorpha which reveal that the number is not fixed in the ground plan of the single subgroups (Cobben 1978). The number of stylet dendrites in Enicocephalomorpha, Dipsocoromorpha, and Coleorrhyncha is presently unclear and needs further investigation with transmission electron microscopy. Cobben (1978) admitted at least the general absence of maxillary dendrites (and likely the appropriate canal) in the ground plan of Pentatomomorpha. The maxillary and mandibular stylets of Enicocephalomorpha as seen with light microscopy are also perforated each by a single duct (fig. 10 of Spangenberg et al. 2013a).

The presence of sensilla at the tip of the labium is a soft character in Hemiptera as this structural unit has often been shabbily treated by various authors. In many species such as *Hydrocyrius* (Kopelke 1978) the sensilla at the labial apex are just labeled as “Sinneshaarfelder”, as “Sinnesstiftchen” in *Aphis* (Weber 1928) and as “tactile hairs” and “stout spines” in *Dysdercus* (Khan 1972). In each case a detailed specification or large-sized figures are absent. In the studies of “Homoptera” of Kramer (1950) and Singh (1971) a documentation of labial sensilla is totally absent. This is in contrast to the present results and to the following studies. The arrangement of labial sensilla in Coleorrhyncha was summarized in detail in Spangenberg et al. (2013a) (see also Brozek [2007] for information to *Xenophyes cascus* [BERGROTH, 1924]). Brozek & Bourgoin (2013) documented 13 different morphological types of sensilla (i.a. multiporous, uniporous, nonporous sensilla; sensilla basiconica;

peg-like, dome-like, cupola-like sensilla) in Fulgoromorpha. They are arranged in a field of 12 to 35 pairs on each side of the labial tip (ground plan condition likely 13 pairs in plant hoppers) whereby the number of pairs is characteristic for the single families (Foster et al. 1983a; Backus 1985; Mora et al. 2001; Brozek & Bourgoin 2013). The numerous labial sensilla in Cicadellidae (Cicadomorpha) are hair-like without pores or the origin in a pit (Tavella & Arzone 2009; Leopold et al. 2003). These sensilla are of mechanosensory type and referring to figure 12 of Leopold et al. (2003) likely arranged in 14 pairs bilateral symmetrically. According to Brozek & Bourgoin (2013) a mechanoreceptive sensillum is indicated by a nonporous condition, whereas a perforated sensillum gives evidence to a chemoreceptive function (see also Chapman RF 2003). The highest morphological diversity of labial sensilla is apparently developed in Fulgoromorpha with menchanoreceptive, chemoreceptive and thermoreceptive function (Foster et al. 1983a; Brozek & Bourgoin 2013).

An additional character not included in the cladistic analysis is the presence of antennal sensilla. The antennal flagellum of Fulgoromorpha is either non-segmented (*Achilixius sandakanensis* MUIR, 1923, Achilixiidae, Liang 2001; *Hyalesthes obsoletus* SIGNORET, 1865, Cixiidae, Romani et al. 2009) or segmented and composed of several subunits (see character state matrix). In Achilixiidae one can distinguish five different morphological types of antennal sensilla, i.a. microtrichia, cuticular denticles, plaque organs ("plate organs or sensilla placodea" in Bourgoin & Deiss 1994), a coeloconic sensillum, and a basal flagellar process (Liang 2001). However, there is apparently a high variability in the morphological characteristic and number of antennal sensilla in Fulgoromorpha with reductions for example in Cixiidae (Romani et al. 2009). The plaque organ is composed of highly folded cuticle which encircles a pore representing the opening of numerous olfactory dendrites (Lewis & Marshall 1970). Antennal sensilla of similar structure, especially the plate organs, were also found in Psyllidae (Moran & Brown 1973). In the later the peg-like sensilla are of chemosensory and likely also mechanoreceptive type. Romani et al. (2009) also suggested that antennal sensilla perceive differences of temperature, humidity and CO_2-concentration. Bromley et al. (1979, 1980) documented also five different types of antennal sensilla (coeloconic, placoid, trichoid, chordotonal, campaniform) for Aphididae. Lewis & Marshall (1970) gave the theory that the plaque organ emerged from a group of sensilla basiconica. This is supported by the grouped presence of six to ten cells/dendrites sharing a single sheath organized in a higher-group. Assuming this organization the fulgoromorph sensilla placodea resembles more the sensillum basiconicum of *Lygaeus kalmii* STÅL, 1874 (Lygaeidae, Pentatomomorpha) than those of Aphididae lacking a folded cuticle and only developed a single group of sensory cells (summarized in Lewis & Marshall 1970). In general, in the antennating groups Sternorrhyncha and phytophagous Heteroptera (Miles 1958) the antennae are longer (with respect to the total length of the head capsule) than in Auchenorrhyncha and Coleorrhyncha.

The latter can only use the labial terminal sensilla for host identifying. Rani & Madhavendra (1995) described also sensilla basiconica (chemoreceptive), sensilla trichodea (mechanoreceptive), and sensilla chaetica (mechano-chemoreceptive) for the pyrrhocorid species *Odontopus nigricornis* STÅL, 1861 (Pentatomomorpha) and sensilla basiconica, sensilla trichodea, and sensilla coeloconica for the pentatomid member *Nezara viridula* (LINNAEUS, 1758) (Pentatomomorpha).

The presence or absence of valves in the salivary pump is an ambiguous character and not included in the cladistic analysis. The classification is also impeded by the size of the specimens and the orientation of the section series (cross sections vs. longitudinal sections). Ammar (1985) listed auchenorrhynchous species with and without valves in the afferent and efferent salivary ducts. Valves are also not clearly documented for Psyllidae and Aleurodidae (Weber 1930). I agree with Weber (1928) that these valves seem to be essential for pumping and sucking and that minute specimen complicate the detection of those structures.

The detection of the epipharyngeal sense organ is also limited by the size of the specimen. This structure is composed of papillae located on epipharyngeal and hypopharyngeal regions and represents likely a ground plan character of Hemiptera (Backus 1988). The epipharyngeal sense organ is associated with the precibarium which was introduced by Backus & McLean (1982) and describes the narrow canal situated between the maxillary food canal and the cibarium *sensu stricto*. The distal opening is referred as “anatomical mouth”. Its origin is apparently epipharyngeal and hypopharyngeal (Backus & McLean 1982). The precibarium of *Macrosteles* (Cicadellidae, Membracoidea, Cicadomorpha) is equipped with 20 chemoreceptive gustatory sensilla (epipharyngeal sense organ) of two different morphological types and a single precibarial valve (Backus & McLean 1982, 1985). The number of 20 precibarial sensilla is likely constant in Cicadomorpha with differences in the exact position (Backus & McLean 1983; Ullman & McLean 1986; Rodrigo & Purcell 2006). The sensilla of leafhoppers are arranged in one distal group (ten D-sensilla) and two proximal groups. The latter consists of eight epipharyngeal P-sensilla and two hypopharyngeal H-sensilla. Both groups of sensilla are separated by the precibarial valve (Backus & McLean 1982). The valve is a tongue-like, hollow, and sclerotized structure in the plane of the epipharyngeal sense organ which is directed caudad (see also Fig. 13). Its base is attached to the epipharynx and builds an internal apodeme (“hinged”) as insertion side for the valve muscle. The distal opening of this apodeme is called the precibarial pit. The valve muscle is clearly separated from the cibarial dilatators (Backus & McLean 1982; Rodrigo & Purcell 2006). The precibarial valve including the apodeme and valve muscle originating on the clypeus is also present in *Philaenus* (Cercopoidea) (Fig. 13). A muscle of the same origin and position is documented for the auchenorrhynchous species *Idiocerus* (22 of Arora & Singh 1962), *Melicharia* (31 of Singh 1971), and *Dictyophara*. However, in the latter species

there is no hint to the precibarial valve or, in the case of *Dictyophara*, it is apparently reduced to a solid portion of cuticle. Consequently, there is a high plasticity in the formation of this character impeding its clarification in the ground plan of Auchenorrhyncha and Hemiptera. However, Backus & McLean (1982) and Backus (1985) suggested that the precibarial valve is indeed part of the ground plan of "Homoptera".

The precibarium of the psyllid *Psylla pyricola* FOERSTER, 1848 (Ullman & McLean 1986) is characterized by 18 chemoreceptive sensilla (ten D-sensilla, six P-sensilla, two H-sensilla) and a flap-like precibarial valve including its apodeme and valve muscle. A valve of similar structure is documented for Aphididae (McLean & Kinsey 1984) and Aleyrodidae (Hunter et al 1996). The set of precibarial sensilla in Aleyrodidae is composed of ten multiple-innervated, uni-porous sensilla (Hunter et al. 1996). The cibarium of white flies is additionally equipped with a sense organ composed of six multiple-innervated, uni-porous chemosensilla on the epipharyngeal region and two uni-porous chemosensilla on the hypopharyngeal portion (Hunter et al. 1996). The 16 multiple-innervated chemoreceptive papillae on the anterior alimentary canal of Aphididae are separated into eight D-sensilla ("anterior papillae"), six P-sensilla ("posterior papillae") and two H-sensilla ("paired papillae in the ventral wall of the food canal") (Wensler & Filshie 1969; McLean & Kinsey 1984).

The cibarial sense organ is also documented for Cicadomorpha, Aphididae, Psyllidae, and Thysanoptera (summarized in Hunter et al. 1996). The general gustatory function of this organ is the main trigger for the acceptance or rejection of a food source (Chapman RF 2003).

Rieger (1976) outlined in detail the epipahrynx of the water bug *Ochterus*. Although a distinct valve is not documented for *Ochterus*, there is also an internal apodeme of the epipharynx and a delicate muscle (KM14) inserting on a plate-like strengthening of the epipharynx. According to Rieger (1976) the muscle KM14 is not capable for efficient dilatation of the cibarium and, thus, apparently involved in the function of the epipharyngeal sense organ. Following this assumption KM14 is likely homologous to the valve muscle. However, as listed in the character state matrix, there seems to be a trend in Auchenorrhyncha of a splitting of the cibarial dilatators muscles. In general, the clarification of the different cibarial dilatators (including KM14) is impeded by the high degree of muscular fusion (e.g. in Dipsocoromorpha). However, a precibarial valve is unambiguously reported for *Lygus hesperus* (KNIGHT, 1917) (Miridae, Pentatomomorpha) (unpublished data in Backus 1985).

The precibarial valve is apparently multi-functional in Hemiptera. On the one hand it is an additional regulator of the amount of ingested fluids, especially in phloem-feeders to "stop" the capillarity of the phloem-sap with positive hydrostatic pressure (Backus & McLean 1982). On the other it influences the allocation of the food stream to the gustatory sensilla of the epipharyngeal sense organ, i.a. pre-sensing by D-sensilla and sensitive-sensing by P-

sensilla and H-sensilla (Backus & McLean 1982). The valve also seals the distal opening of the cibarium in Cicadomorpha (Backus & McLean 1982; Ullman & McLean 1986), whereas in Sternorrhyncha it is only capable of closing the hypopharyngeal valve receptacle which then seals the entrance of the food pump (McLean & Kinsey 1984; Ullman & McLean 1986). Summarizing, the presence of the precibarial valve including the valve muscle is likely a ground plan character of Hemiptera with reduction in Coleorrhyncha and Heteroptera (but see Rieger 1976 above for Nepomorpha).

Rodrigo & Purcell (2006) outlined a second valve (cardiac or esophageal valce) which is located between the esophagus and midgut. It is opened passively and prevents the back-flow of ingested saps from the midgut to the esophagus during dilation and suction of the cibarium. The cardiac valve is likely a part of the hemipteran ground plan and at least reported for Cicadomorpha, Aphididae, Psyllidae and also Thysanoptera (summarized in Rodrigo & Purcel 2006). It is also described for *Troctes* (*Liposcelis*) *divinatorius* (Noland 1924).

The filter chamber is not directly a cephalic character but linked with the ingestion and processing of food in Hemiptera. It is represented by a modified portion of the midgut which rapidly transmits surplus water to the hindgut and, thus, concentrates the ingested liquids (Ammar 1985). The filter chamber is documented for xylem- and phloem-feeding auchenorrhynchous Cicadoidea and Cercopidae (Ammar 1985; Wiesenborn 2004), whereas it is absent in Fulgoromorpha (O'Brien & Wilson 1985), Coleorrhyncha (Pendergrast 1962), and Heteroptera (e.g. Schlee 1969). The absence in the mesophyll-feeding and carnivorous groups is likely due to the non-necessity of concentrating the ingested liquids as they are inherently rich in nutrients. Similar but rather complex filtering devices are reported for some Aleyrodoidea, Aphidoidea, and Psylloidea (summarized in Ammar 1985).

Between the bases of the antennae of *Cacopsylla* there is each a globular gland of unknown homology so far not documented before (Fig. 28). The gland is composed of few cubic cells arranged around an ovoid atrium. A simple duct runs from this atrium to the ventral base of the pedicellus with the presuambly external opening.

Heteroptera

The monophyly of true bugs is well supported (BS 7), but just characterized by nine homoplasies. With respect to polyphyletic Nepomorpha and paraphyletic Dipsocoromorpha the phylogeny of Heteroptera as shown by the present study is highly controversial and uncertain. Spangenberg et al. (2013b) summarized different heteropteran phylogenies and tentatively showed the hypothesis of Wheeler et al. (1993) (Enicocephalomorpha + (Dipsocoromorpha + (Gerromorpha + (Nepomorpha + (Leptopodomorpha + (Pentatomomorpha + Cimicomorpha)))))) has been proved at best. A basal position of

Heteroptera is so far only accepted by Boulard (1988). However, a unit of Hemiptera excl. Heteroptera (low Bremer Support 1) is in contrast to the majority of molecular and morphological data (see Fig. 2) and requires further investigation with an expanded morphological character matrix or should displayed as an unresolved trichotomy (see Friedemann et al. 2013). Preliminary results of 1KITE (Misof et al. subm.) confirmed instead a basal position of Sternorrhyncha supporting the clade Euhemiptera (see also Wheeler et al. 1993).

Parsons (1974) introduced a landmark “point c” as articulation point of the mandibular lever with the head capsule which is situated at the proximal end of the cleft separating mandibular from maxillary plates. It is located at the level of the anterior tentorial pits or at the level of the compound eyes in “Homoptera” and far ventrad these landmarks at the anterior region of the head capsule in Heteroptera (Parsons 1974). This assumption is confirmed for Heteroptera by our taxon sampling (see character state matrix). However, with respect to Fulgoromorpha (Kramer 1950; Singh 1971), *Idiocerus* (Cicadellidae, Membracoidea, Cicadomomorpha) (Arora & Singh 1962) and *Lepyronia* (Cercopidae, Cercopoidea, Cicadomorpha) (Kramer 1950) the separation of “Homoptera” and Heteroptera according only to point C is ambiguous.

In the ground plan of Heteroptera the tentorium is generally considered as absent (e.g. summary in Grimaldi & Engel 2005). There are, however, apparently taxa retained a more primitive condition with vestigial anterior tentorial arms such as in *Nepa* (Hamilton 1931), *Notonecta* (Bourgoin 1986b) (both Nepomorpha), and *Saldula* (Leptopodomorpha) (“dorsal apodeme” of Parsons 1963).

The distribution of sensilla at the tip of the labium within Heteroptera is considered as highly variable. In the studied taxa terminal labial sensilla are at least present in some members of Nepomorpha, Cimicomorpha and Pentatomomorpha. Brozek (2008) reported at least five different morphological types of labial sensilla (i.a. basiconic sensilla, papillae sensilla, ribbon-like sensilla, pit sensilla, sensilla chaetica) with number and pattern characteristical for the single nepomorph families. Even 24 morphological different sensilla are present on the entire labium of Nepomorpha (Brozek 2013a). Sensilla of water bugs are of chemoreceptive or mechanoreceptive type (except Aphelocheridae) and arranged bilaterally symmetrical in a group of eight to 14 (Brozek 2008, 2013a). The terminal labial sensilla of the genus *Dysdercus* (Pyrrhocoridae, Pentatomomorpha) are arranged in group of ten to 13 laterad the labial groove (Schoonhoven & Henstra 1971; Peregrine 1972a; Gaffal 1981). Schoonhoven & Henstra (1971) distinguished four different morphological types of sensilla basiconica and sensilla trichodeum (sensilla chaetica in Gafall 1981). At least three of four types of sensilla basiconica are multiple-innervated and uniporous suggesting a chemoreceptive function (Schoonhoven & Henstra 1971; Gaffal 1981). Additionally, there are sensilla basiconica and sensilla chaetica which are supplied both by mechanoreceptive and chemoreceptive den-

drites (mechano-chemoreceptive function) (Gaffal 1981). The arrangement and number of labial sensilla of *Blissus leucopterus leucopterus* (SAY, 1832) (Blissidae, Pentatomomorpha) is similar to those of *Dysdercus* (Baker et al. 2008). Baker et al. (2008) described uniporous peg sensilla and a single sensillum chaeticum with mechano-chemosensitive function (see also Anderson et al. 2006). The last species should be considered in the list of pentatomorph members is *Eocanthecona furcellata* (WOLFF, 1811) (Pentatomidae) (Rani 2009). The set of terminal labial sensilla comprises four distinct morphological types including mechanosensitive or chemosensitive function (Rani 2009). As documented above, the number of terminal labial sensilla in the ground plan of Pentatomomorpha is not determined (see also Rani & Madhavendra 1995). The diversity of sensilla in Reduviidae (Cimicomorpha) comprises 13 different morphological types (Brozek & Chlond 2010). The sensilla reported in the latter study are of mechanosensitive or chemosensitive function. Singh et al. (1996) documented the labial sensilla of the cimicomorph *Cimex* (Cimicidae). They gave information to 20 terminal sensilla basiconica with mechanoreceptive or chemoreceptive function.

Wenk et al. (2010) documented one dorsal and one ventral efferent salivary duct for the hematophagous bug *Rhodnius prolixus* STÅL, 1859. The ventral duct is situated in the distal socket-like part of the hypopharynx while the dorsal one lies upon (fig. 3b of Wenk et al. 2010). The dorsal efferent duct supplies the salivary canal of the maxillae directly with saliva whereas the ventral one opens into the labium. The saliva of the latter likely lubricates the stylets or cleans them after pulling out of the host tissue (Wenk et al. 2010). The salivary complex of the basal considered *Systelloderes* is equipped as well with one efferent duct situated on the dorsal side of the hypopharyngeal socket (Spangenberg et. al 2013b.). However, there is no hint to a ventral duct as the socket is solid and situated far ventrad the origin of the maxillary canal. Wenk et al. (2010) referring to Benwitz (1956) and Parsons (1963, 1968) considered two efferent salivary ducts as well for *Corixa* and *Lethocerus*, respectively. However, both authors just described one single efferent duct, admitting that Benwitz's (1956) figure 16 and Parsons's (1968) figure 10 are similar to that of Wenk et al. (2010, fig. 3b). Barth's (1952a,b, fig. 23) scheme of the salivary pump for *Triatoma* shows the same condition as for *Rhodnius* (Wenk et al. 2010, fig. 3b), but only the dorsal salivary duct ("Ausfuehrgang der Speichelpumpe") is explicitly mentioned. The ventral duct is described as a secondary lumen of the pumping chamber which can be closed by interlocking of the distal edges of these invaginations (Barth 1952a, fig. 23). Additionally, it seems essential that there is a valve at the distal end of the ventral salivary duct to regulate the flow of the saliva, either into the maxillary salivary canal (valve closed) or into the labium (valve opened). Such a structure is not documented by Wenk et al. (2010). Consequently, the homology of the ventral duct of Wenk et al. (2010) is doubtful or at least likely a unique specialization of the hematophagous assassin bugs. In general, the hypopharyngeal socket bearing the pumping

chamber is described as ventral duct for *Dipetalogaster maxima* (UHLER, 1894), *Panstrongylus megistus* (BURMEISTER, 1835) (both Reduviidae), *Pyrrhocoris apterus* (LINNAEUS, 1758) (Pyrrhocoridae) and *Troilus luridus* (FABRICIUS, 1775) (Pentatomidae) by Wenk et al. (2010) which is inconsistent with previous studies on Heteroptera (e.g. Cranston & Sprague 1961; Parsons 1962; Khan 1972; Rieger 1976).

The tripartite apex of the labium including a closing lid ventrally is also a potential autapomorphy of Heteroptera (with reduction in *Hypsipteryx, Hydrocyrius, Saldula* and *Dysdercus*). Rani & Madhavendra (1995) reported an apical plate flanked by two lobes in another specimen of Pyrrhocoridae than *Dysdercus* (*Odontopus nigricornis* STÅL, 1861) and additionally for the pentatomid species *Nezara viridula* (LINNAEUS, 1758). A tripartite apex is also present in the genus *Blissus* (Blissidae, Lygaeoidea) (Anderson et al. 2006, figs. 1D, 2D, 3D; Baker et al. 2008, fig. 2). This reveals that the apical plate is likely present in the ground plan of Pentatomomorpha as well. In this context, Wenk et al. (2010) also documented a ventral lid at the apex of the labial rostrum for *Rhodnius, Triatoma, Dipetalogaster, Panstrongylus*, *Pyrrhocoris,* and *Troilus* (see also Cobben 1978). Wenk et al. (2010) speculated if this structure is functionally connected to the second ventral salivary duct. This theory can be at least rejected for Enicocephalomorpha as the ventral salivary duct is absent (see above). There is also no intrinsic musculature for the movement of this lid (Cobben 1978). Furthermore, it is questionable if a completely sealing of the labial groove on its entire length is possible which would be essential for the functionality suggested by Wenk et al. (2010). According to Cobben (1978) the lid ("apical plate") or the tripartite apex is likely responsible for cleaning the maxillae after feeding or as manipulating organ for the direction of protrusion of the feeding stylets. Even the occurrence of the lid within a single family is occasionally variable. In Saldidae (Leptopodomorpha) for example it can be present (e.g. *Aepophilus,* Cobben 1978) or absent (*Saldula,* Parsons 1962). In Pentatomomorpha there are also members with and without the lid (summarized in Cobben 1978).

Sternorrhyncha

Sternorrhyncha are confirmed as monophylum (e.g. Strümpel 2005c; Beutel et al. 2013a) although with low Bremer Support (2) and only the presence of seven homoplasious apomorphies. At least the monophyly of the subgroups Aleyrodoidea (BS: 3), Coccoidea (BS: 8), and Psylloidea (BS: 2) is certain and compatible with the hypotheses of von Dohlen & Moran (1995), Cook et al. (2002), Gullan & Cook (2007), and Cryan & Urban (2012). With respect to von Dohlen & Moran (1995), Cook et al. (2002), and Gullan & Cook (2007) also the monophyly of Aphidoidea appears proved. In contrast, there is an ongoing debate concerning the internal sternorrhynchan relationships. The present study gives evidence to

(Aleyrodoidea + (“Aphidoidea” + (Coccoidea + Psylloidea))). One alternative concept instead favors the presence of the clades Psyllomorpha/Psylliformes (= Psylloidea + Aleyrodoidea) (Strümpel 2005c; Friedemann et al. 2013) and Aphidomorpha/Aphidiformes (= Aphidoidea + Coccoidea) (Campbell et al. 1994; von Dohlen & Moran 1995; Strümpel 2005c; Cryan & Urban 2012; Friedemann et al. 2013). Potential apomorphies of Psyllomorpha are only non-cephalic (i.a. not supported in the present study) and restricted to the presence of a sperm pump, a ring muscle layer of the ductus ejaculatorius, the reduction of the two proximal abdominal segments, broadened distal coxae and the presence of pedunculate eggs (summarized in Strümpel 2005c). Support for Aphidomorpha so far is either based on molecular data (e.g. Campbell et al. 1994; Cryan & Urban 2012; 1KITE in Misof et al. subm.) or to find in the reduced ovipositor, the non-stalked eggs, and the common straight line of subcosta, radius, media, and cubitus (for summary see Strümpel 2005c). Ambiguous homoplasious apomorphies for Aphidomorpha listed by Friedemann et al. (2013) are the absence of arolium and pulvilli. Enforcing Aphidomorpha with the present taxon sampling and character matrix additionally yielded the homoplasious characters *presence of a clypeal suture*, *presence of 0lax11*, and *the origin of 0lax14 on the cranium.* Another hypothesis clearly indicates the non-monophyly of Psyllomorpha with either Psylloidea as basal sternorrhynchan stem group (Campbell et al. 1994; Cryan & Urban 2012) or Aphidomorpha (von Dohlen & Moran 1995) or Aleyrodoidea (present study; 1KITE in Misof et al. subm.).

In Aleyrodoidea there is each a set of seven terminal labial sensilla arranged symmetrically with respect to the labial groove (Rosell et al. 1995; Walker & Gordh 1989; Bährmann 2002). Walker & Gordh (1989) documented single and multiple innervations of sensilla which is a hint for chemosensory or mechano-chemosensory function. In contrast, the distal labial segment of Aphidoidea is equipped with eight pairs of sensilla just fulfilling mechanosensory function for detection of surface contact and texture (Forbes, 1977; Wensler 1977; Backus 1988). The apex of the rostrum of *Diaphorina citri* KUWAYAMA, 1908 (Psyllidae, Psylloidea) bears four bilaterally symmetrical pairs of conical sensilla with ambiguous clarification of chemosensory or mechanosensory function (Garzo et al. 2012). Sensilla of chemosensory and mechano-sensory type can be found on the labial tip of *Kerria lacca* (KERR, 1782) (Tachardiidae, Coccoidea) (Ahmad et al. 2012). In this species there are five pairs of slender sensilla around the distal opening of the labium. In the coccoid species investigated in the present study, sensilla at the terminal labial segment are apparently absent or coated by wax-like incrustations. However, five bilaterally symmetrical sensilla are documented for *Pseudococcus* by Weber (1929b, fig. 8B) assuming this is a ground plan character for Coccoidea.

An apomorphic character apparently overlooked in the last decades of hemipteran research is the “acrostyle” of Aphididae (Aphidoidea) (Uzest et al. 2010; Garzo et al. 2012).

This structure is a thin layer of compressed cuticle that coated the inner wall of the fused maxillary salivary canal and food canal at the level of the labial tip (Uzest et al. 2010). It is only seen by transmission electron micropscopy or epifluorescence microscopy combined with the labeling of P2-GFP (Uzest et al. 2010). The acrostyle is likely essential in the transmission process of plant viruses. However, the function in aphids is presently unclear. Uzest et al. (2010) argued that the compressed cuticle strengthened the maxillary apex and, thus, shows increased resistance during piercing of phloem vessels. Furthermore, the acrostyle may influence the fluid dynamics by changing the hydrophobicity or hydrophilicity. A third putative function listed by Uzest et al. (2010) is the protein binding capacity. Therefore, the inner walls of the common duct restrain sucking-inhibiting proteins which will be flushed away by the next saliva output. The acrostyle may also play a role in the building of the salivary sheath by accumulation of proteins which are capable of gelling and theirs quite suddenly release during contact with watery saliva or air (Uzest et al. 2010).

Strümpel (2005c) outlined the presence of a “triommatidium” (knob located directly posterad the compound eye and bearing three ommatidia) as an additional cephalic autapomorphic character for Aphidoidea. However, this feature is not explicitly distinguished in *Macrosiphum* (Singh 1971) and *Dactylosphaera* (Breider 1952). So far the only reliable documentation in the present taxon sampling is restricted to *Aphis* (Weber 1928).

According to Singh (1971) the crumena has developed from the labial groove in the second labial segment, whereas Weber (1929a) described the crumena as invagination of the hypodermis between hypopharynx and labium. The muscular configuration of the crumena within Psylloidea is highly variable. In *Diaphorina* (Singh 1971) the retractor of the crumena is well developed, it is reduced to delicate fibers in *Cacopsylla* and totally absent in *Psylla* (Weber 1929a). The present study strongly disagree with Weber (1929a,b, 1935) who used the term “crumena” in Psyllidae and Coccidae as well as in Aleyrodidae. In the last group the crumena resembles the unpaired apodeme of the second labial segment reaching far proximad. This structure is not able to host the feeding stylets as the true sac-like crumena of pysllids and coccids. However, the hollow sclerotized rod in white flies could be a preadaptation for the development of the crumena which is located in a similar position.

The most peculiar apomorphy of the head capsule of Aleyrodidae is the division of the compound eye into a ventral and dorsal part (e.g. Weber 1935; Singh 1971). Gill (1990) outlined the absence of the ocular division is an important feature for the classification of single genera or species, without clarifying what character state is the primitive one. The number of ocelli of Aleyrodidae is apparently two in the ground plan with a third frontal ocellus at least in *Paraleyrodes* (Gill 1990). The muscular configuration of the maxillary lever within white flies is highly variable. It is equipped with a retractor muscle in *Trialeurodes* (Weber 1935) and with a protractor muscle in *Aleurolobus* (Singh 1971). In *Aleyrodes* the partitions of the max-

illary retractor inserts directly on the maxillary base, just laterad the attachment of the maxillary lever. This configuration is different from that documented by Weber (1935, Textabb. 3a). A similar case was observed for the maxillary protractor of *Cacopsylla*. In this species the maxillary protractor inserts also laterad the attachment of the maxillary lever without direct contact. However, the opposite condition is reported by Weber (1935, Textabb. 3b) for *Psylla*. One can speculate if these different configurations concerning the relation of the maxillary lever to the maxillary protractors or retractors are due to individual variability. Apparently, the maxillary lever and its muscle attachment site are not essential for the direct lacinial protraction or retraction.

"Auchenorrhyncha", Coleorrhyncha

The present study suggests a clade ((Fulgoromorpha + Coleorrhyncha) + Cicadomorpha). Its significance is reduced by the low Bremer Support of the entire unit (1), (Fulgoromorpha + Coleorrhyncha) (1) and only the presence of few homoplasious apomorphies supporting these nodes. The potential clade Heteropterodea/Prosorrhyncha (= Coleorrhyncha + Heteroptera) would be supported by only a single homoplasy (maxillary lever without muscle attachment side). Enforcing Neohemiptera (= Fulgoromorpha/Archaeorrhyncha + Prosorrhyncha) (e.g. Sorensen et al. 1995; Ouvrard et al. 2000) yielded also only homoplasious apomorphies (origin of antennae below eyes; maxillary lever without muscle attachment side). A placement of Coleorrhyncha close to Auchenorrhyncha and Sternorrhyncha was suggested recently by the first cytogenetic study of Peloridiidae (Grozeva et al. 2014). The branching pattern Fulgoromorpha + Coleorrhyncha is supported additionally by two molecular data sets of Cui et al. (2013). These findings provided new evidence for the paraphyly of Auchenorrhyncha. However, preliminary results of the analysis of transcriptomic data with a limited hemipteran taxon sampling rendered at least Auchenorrhyncha as monophyletic with Coleorrhyncha as sister group (1KITE in Misof et al. subm.). Thus, the monophyly or paraphyly of Auchenorrhyncha should be considered as an open question.

The monophyly of the three subgroups instead is sufficiently confirmed: Fulgoromorpha (BS: 1; three apomorphies including a single non-homoplasious character) (see also Campbell et al. 1994; von Dohlen & Moran 1995; Cryan & Urban 2012), Coleorrhyncha (BS: 5, five apomorphies including four non-homoplasious characters) (see also Ouvrard et al. 2000; Burckhardt 2009), and Cicadomorpha (BS: 4, four apomorphies, including two non-homoplasious characters) (see also Campbell et al. 1994; von Dohlen & Moran 1995; Cryan & Urban 2012). Cephalic features are limited to reconstruct group-internal relationships. *Hackeriella* and *Hemiodoecus* were placed as sister groups as also documented by Burck-

hardt (2009). The latter study, considering also thoracal and genitalia characters, however, did not show *Pantinia* and *Peloridium* as basal lineages.

The cicadomorph Cercopoidea, Cicadoidea, and Membracoidea are regarded as monophyletic units (e.g. Campbell et al. 1994; Cryan & Urban 2012). The present topology showed Cercopoidea is paraphyletic, with respect to the former studies a rather unlikely condition. The present branching pattern ("Cercopoidea" + (Cicadoidea + Membracoidea)) is also supported by Campbell et al. (1994), whereas Cryan & Urban (2012) and Zhang & Dai (2012) favored (Membracoidea + (Cicadoidea + Cercopoidea)).

Singh (1971) described a set of muscles "44" which connects the pronotum with the posterior tentorial arm in *Hemiodoecus* (Idvmx1). A similar set "45" runs from the pronotum to the corpotentorium and is only present in *Aleurolobu*s and *Macrosiphum* studied by Singh (1971) (Idvmx4). However, confusingly, Singh (1971) labeled in his fig. 50 a muscle 45 for *Hemiodoecus*, although it should be absent in this species. I interpreted this as a typing error which was not yet detected in Spangenberg et al. (2013a) and should corrected there. This also concerns muscle sets 51 (Ivlm3) and 52 (Idvmx3), which are not explicitly described in text for *Platypleura* (in contrast to all other species studied by Singh 1971) but which are labeled in his figs. 9 and 10.

A remarkable structure within Hemiptera is the Evans organ. It is a part of the maxillary plate and present in "many, and possibly most, Homoptera-Auchenorrhyncha" (Evans 1973). So far this pit-like structure with or without a palp-like process is documented for Cercopoidea (Machaerotidae, *Chaetophyes compacta* [WALKER, 1851]), Cicadelloidea (Eurymelidae, *Cornutipo tricornis* [EVANS, 1934]), Cicadoidea (Cicadidae, *Parnkalla muelleri* [DISTANT, 1982]), Membracoidea (Cicadellidae synonym Jassidae, *Trocnada dorsigera* WALKER, 1858; *Stenocotis depressa* [WALKER, 1851]; *Monteithia anomala* EVANS, 1968; *Cicadella spectra* [DISTANT, 1908]; *Ledropsis crocina* DISTANT 1917; *Cephalelus punctatus* EVANS 1939; *Zyginidia pullula* [BOHEMAN, 1845]; *Empoasca vitis* GOETHE, 1875; *Graphocephala fennahi* YOUNG 1977), and Fulgoridae (*Scolops pungens* [GERMAR, 1830]) (Evans 1973; Tavella & Arzone 1993). Tavella & Arzone (1993) pointed out the unclear homology of the Evans organ which is interpreted either as maxillary gland or sense organ or part of the maxilla. The Evans organ is not explicitly mentioned and documented in other or the same members of Cicadidae (*Tibicina septendecim* [LINNAEUS, 1758]; *Platypleura octoguttata* FABRICIUS 1798), Cercopidae (*Lepyronia quadrangularis* [SAY, 1825]; *Ptyelus nebulosus* [FABRICIUS, 1794]), Membracidae (*Ceresa bubaluls* FABRICIUS, 1794; *Oxyrhachis tarandus* [FABRICIUS, 1798]), Cicadellidae (*Aulacizes irrorata* [FABRICIUS, 1794]; *Idiocerus* atkinsoni LETHIERRY, 1889; *Kolla mimica* [DISTANT, 1908]), Flatidae (*Melicharia quadrata* MELICHAR, 1903) and Fulgoridae (*Scolops pungens* [GERMAR, 1830]) (Kramer 1950; Arora & Singh 1962; Singh 1971). It is absent in *Philaenus* and *Dictyophara*. Bourgoin (1986a) doc-

umented the Evans organ for *Hemiodoecus*. However, it is obviously not present in the specimen studied by Singh (1971) and Peloridiidae examined in this study. Thus, this structure should be only tentatively considered as potential synapomorphy of Coleorrhyncha + Auchenorrhyncha.

In Fulgorormorpha (except Fulgoridae) an additional sense organ is present each at the distal lateral sides of the fourth labial segment ("labial palpi" of Sogawa 1977, 1982; "multi-lobed receptor" of Foster et al. 1983a; "latero-subapical labial sensillum" of Liang 2005; "subapical labial sensory organ" of Brozek & Bourgoin 2013). This organ is composed of a pit which is the origin of multiple-innervated and multiporous branched sensilla (Foster et al. 1983a). The branching pattern and its structure (i.a. tubular, cone-like, or placoid) are highly variable and apparently characteristic for the single families (Brozek & Bourgoin 2013). The multiple-lobed receptor is presumably an apomorphy of Fulgoromorpha (with secondary loss at least in Fulgoridae) and absent in Cicadomorpha and Hemiptera (Cobben 1988; Brozek & Bourgoin 2013). However, Brozek & Bourgoin (2013) stated a similarity between the auchenorrhynchous multiple-lobed receptor and the "baton-shaped structure" of the heteropteran *Cimex hemipterus* FABRICIUS, 1803 (Cimicidae) (Singh et al. 1996). As a drawback there is only a SEM graph of poor quality (Singh et al. 1996, fig.3E) of the latter structure and a comprehensive description in the text is absent. Additionally, *Cimex* was air-dried at room temperature for 24 hours which can induce shrinking artifacts and impede possible homologization. More reliable is the comparison of the multiple-lobed receptor with the multiple-lobed sensilla in the predatory *Eocanthecona furcellata* (WOLFF, 1811) (Pentatomidae, Pentatomomorpha) (Rani 2009). In contrast to the multiple-lobed receptor, these branched sensilla are located at the tip of the labium and do not originate in a common pit (Rani 2009). The presence of the multiple-lobed receptor is likely linked with the host-plant preference (see Brozek & Bourgoin 2013) or it could serve as a detector for humidity (see Rani 2009).

Another potential autapomorphy of Fulgoromorpha is the presence of the Bourgoin's organ ("organe sensorial basal du flagella") (e.g. Bourgoin 1985; Bourgoin & Deiss 1994; Romani et al. 2009). This is a sensory structure which is located at the base of the third antennal segment (Bourgoin 1985). It is composed of a pipe system with a sensory denticle, a single setum and an atrium with the opening surrounded by a fringed membrane (Bourgoin 1985; Bourgoin & Deiss 1994). The Bourgoin's organ is absent in *Philaenus* and apparently also in other Cicadomorpha.

4.2 Evolution of cephalic characters

“Psocodea”

Acercarian species occupy a very broad spectrum of habits ranging from terrestrial over limnological habitats till to parasitism on mammals and birds. This is reflected in an enormous variety of feeding mechanism influencing the head shape, the structure and muscular configuration of the mouthparts. Psocoptera are relatively close to the original omnivorous life style and representing the most primitive and basal group of acercarian insects. Consequently, the modifications in comparison to a generalized orthognathous insect are limited. Although stylet-like or chisel-like laciniae are arguably an autapomorphy of Acercaria, their function differs fundamentally between Pscocoptera on the one hand and Hemiptera and Thysanoptera on the other. Instead of piercing host tissues the chisel-shaped laciniae is equipped with three strong apical teeth and acts as a drill hammer and break up food. The loosened particles are transported by shovel-like movements of the labrum to the mandibles (incisivial region) for final crushing (von Kéler 1966b). This shows that the psocopteran labrum is essential for food uptake whereas it is not involved in this process in Hemiptera. The galeae push the crushed particles further to the molar region of the mandibles (von Kéler 1966b). In contrast to Hemiptera and Thysanoptera the psocopteran labium is not modified (i.a. bended or shortened) during feeding (von Kéler 1966b). There is substantial disagreement concerning the functionality of the epipharyngeal “pestle” and the corresponding hypopharyngeal sitophore or “mortar” of Psocoptera, Amblycera and Ischnocera. Due to the comparison with a mortar and pestle apparatus it is apparently essential for grinding up solid food particles or keratin-rich feathers and hairs (Snodgrass 1944; Matsuda 1965). However, von Kéler (1966b) considered the absent documentations of the linkage of the pestle and mortar on the one hand and the absence of food particles in the mortar on the other (confirmed in the present study). Von Kéler (1966b) documented for single species of Ischnocera a hollow epipharyngeal “pestle” and hypothesized that the entire complex acts a pump for creating a negative pressure. This forces the labium to press against the hypopharynx and to excrete saliva from the salivarium into the salivary cavity (see also the meaning of negative pressure for water-vapor uptake).

Psocodea developed a unique water-vapor uptake facility within Acercaria which is clearly an adaptation to dry habitats in dirt (Psocoptera) or feathers and hairs (Ischnocera and Amblycera). The device is composed of a pair of hypopharyngeal oval lingual sclerites locating between the distal margins of the labrum and labium and equipped with the hypopharyngeal retractor muscle, a hypopharyngeal membrane spread between the lingual sclerites, an epipharyngeal sclerite equipped with a powerful clypeo-epipharyngeal muscle,

and a pair of tubular filaments perforating the cibarial sclerites (Rudolph 1982, 1983). Water-vapor uptake is achieved by protrusion of the lingual sclerites to a folded out position which stretches the hypopharyngeal membrane. Its surface is capable to attract water in the case of “high humidities above the critical equilibrium humidity” (Rudolph 1982). The thin film of water-vapor condensation is drain off through the tubular filaments into the cibarium. The essential negative pressure is caused by the contraction of the clypeo-epipharyngeal muscle (Rudolph 1982, 1983).

Phthiraptera display a broader variety of mouthpart structures than Psocoptera. Amblycera and Ischnocera (except *Trochiloecetes*) retained the traditional biting mandibles, whereas those of Rhynchophthirina are rotated around 180° and operate laterally (Weber 1969). According to Clay (1949) the evolution of piercing mouthparts has taken place twice independently within Phthiraptera, i.a. in two genera of Amblycera and in Anoplura. *Trochiloecetes* (Ricinidae, Amblycera) is apparently a key taxon within chewing and biting Amblycera. The genus is characterized by the typical chisel-shaped laciniae and non-stylet-like mandibles but equipped additionally with two fused feeding stylets evolved from the “Vorderarme des Cibarialsklerites” (posterior arms of the hypopharynx) (Haub 1983). In contrast, the anopluran hypopharyngeal stylet has evolved not from the dorsal hypopharynx as in Amblycera but from its ventral portion (Haub 1983). The hypopharyngeal stylet as the chief piercing organ of *Trochiloecetes* is either moved actively by solely contraction of the M. hypopharyngo-mandibularis or passively by entire head movement and additional fixation through the mandibular adductors and abductors (Haub 1983). Labrum, pulvini and labium seal between the preoralcavity and the skin of the hummingbird (the host) so that blood flows passively into the mouth (Haub 1983). Haub (1983) also considered an anticoagulant function of salivary and/or lacinial secretions.

In Anoplura the “ontogeny of the mandibular and maxillary appendages has been retarded and repressed and that of hypopharynx and labium accelerated and modified to form the characteristic trophic sac and hypopharyngeal and labial stylets” (Heming 1980). These modifications lead to a unique sucking mechanism which is more complex than that of *Trochiloecetes*. All maxillary subunits except the galea and the lacinia (only *Hybophthirus*) are reduced. The ventral parts of the galeae act as guiding devices for the piercers (see below) (von Kéler 1966a; Tröster 1990a). The mandibles are shifted craniad and theirs articulations is in or anterad the level of the hypopharyngeal tip. In contrast to the orthopteroid type, the mandibles are divided into a globular to flattened ventral part and a flattened to half-pipe dorsal region with the mesal incisivial parts forming a closed canal for the transport of liquids (e.g. von Kéler 1966a; Tröster 1990a,b). The labium is fused with the pleuro- and hypostomal margin of the head capsule and forms a smooth cone-shaped entitiy together with the haustellum (von Kéler 1966a). Labial palps are absent. The most remarkable character of

Anoplura is the presence of a “sting”. It is composed of the dorsal piercing bristle (ventral part of the hypopharynx), the ventral piercing bristle (prementum) and the median piercing bristle (e.g. Matsuda 1965). The origin of the median salivary stylet is either hypopharyngeal (Schölzel 1937; Ramcke 1965) or labial (Stojanovich 1945; Young 1953). The “sting” is hosted in a piercer sheath formed by the dorsal part of the hypopharynx dorsally and the ventral prementum ventrally (Tröster 1990a). This entity is supported by a dorsal guiding device developed from the ventral hypopharynx and an additional lateral one with labial origin in (*Haematopinus* + *Hybophthirus*) (e.g. Tröster 1990a). Tröster (1990a) suggested that *Hybophthirus* shows a primitive mouthpart condition within Anoplura and the mandibles and primary piercing device. Thus, the “piercing bristles consisting of the ventral part of the hypopharynx and the prementum are the secondary piercing devices of the Anoplura“ (Tröster 1990a).

The feeding of Anoplura is more complex than that of Hemiptera (see 4.3). In the latter piercing and sucking are combined and the feeding stylets stay in the insertion side during feeding (von Kéler 1966a). Anoplura in contrast first anchor the head capsule by protrusion of the haustellum into the host tissue with simultaneous sealing of the piercing device (Ramcke 1965). In a next step the hypopharyngeal, salivary and labial piercer enter the blood vessel by alternating movement, saliva is injected by the median salivary stylet (Ramcke 1965). After piercing the bristles are withdrawn and the out flowing blood is taken by the mandibles and galea (*Hybophthirus*, von Kéler 1966a) or the hypopharyngeal stylet and the mandibles (*Haematopinus*, Ramcke 1965) with support of the sucking cibarium (Ramcke 1965). The obturaculum enables a more extended protrusion of the piercers by an anterior shift of the origin of the retractors 0la8 and 0hy4 in *Haematopinus* (Ramcke 1965), and a hermetic sealing of the lumen of the head againt the lumen of the preceding body in *Hybophthirus* (Tröster 1990a). In contrast to Hemiptera the maxillary glands of Anoplura act not as secretory organs (e.g. Qadri 1949; Linder 1956) but are responsible for pressure balance. This is related with the shortening of the piercer sheath caudally during protrusion of the bristles (Tröster 1990a). The shortening in turn resulted in a displaced volume of the piercer sheath (air in *Hybophthirus*, Tröster 1990a; haemolymphe in *Haematopinus*, Ramcke 1965) which then gets in the maxillary glands for pressure balance. The filled maxillary glands apparently have also a negative feedback effect of the protrusion of the piercers by pinching off theirs musculature (Ramcke 1965).

The feeding mode of Rhynchophthirina is presently not fully understood. The rotated mandibles (180°) penetrate the host tissue and blood is sucked up by the rostrum. Specialized piercing organs for injuring blood vessels are not developed (Weber 1939, 1969). The ingestion of blood is superficially similar to that of Ixodida (e.g. Mehlhorn & Piekarski 2002).

Condylognatha

In the hemipteroid assemblage piercing mouthparts evolved for the third time within Acercaria. Hamilton (1981) listed three putative stages which are essential for the evolution of a biting-chewing orthopteroid or “mandibulate” ancestor to a piercing-sucking hemipteran insect. In the first stage the cibarial dilatator(s) and their clypeal origin are modified by a distinctly enlargement (note that the “frons” of Hamilton [1981] is actually the morphological clypeus, see Yoshizawa & Saigusa [2003]). The enlargement of the (post)clypeus is just indicated in Psocoptera and developed further in the most extreme condition in the xylem-feeding groups of Cicadomorpha (Yoshizawa & Saigusa 2003). The enlarged cibarial dilatators are a preadaptation to achieve the essential high suction pressure in Hemiptera and Thysanoptera (Yoshizawa & Saigusa 2003). Yoshizawa & Saigusa (2003) considered the enlargement of both the cibarial dilatators and the (post)clypeus as autapomorphy of Paraneoptera. The enlargement of the postclypeus in Hemiptera is linked with its dorsal extension (Yoshizawa & Saigusa 2003) which is best seen in Cicadomorpha (Auchenorrhyncha) (e.g. Kramer 1950; Singh 1971). Yoshizawa & Saigusa (2003) suggested the dorsal extension of the clypeus as a ground plan character of Hemiptera, Psocoptera, and Thysanoptera evolved independently. It is not apparent why this should not be also a character of an acercarian progenitor. Additionally, the clypeal enlargement and extension is absent in the prognathous, presumably basal heteropterans Enicocephalomorpha, Dipsocoromorpha, and Gerromorpha (Spangenberg et al. 2013b), and reduced in sternorrhynchous Aphididae, Aleyrodidae, and Psyllidae (e.g. Weber 1928, 1929a, 1935). In Thysanoptera the postclypeus is indistinguishably fused with the frons (e.g. Mickoleit 1963). Consequently, the dorsal extension cannot be determined exactly as done by Yoshizawa & Saigusa (2003). It is obvious that the clypeus of Psocoptera is distinctly enlarged (e.g. Badonnel 1934; Yoshizawa 2005), but in its spatial restriction it is similar to an orthopteroid insect (e.g. Matsuda 1965). This is in contrast to the statement of Yoshizawa & Saigusa (2003) that the dorsal extension of the clypeus is part of the psocopteran ground plan.

The modifications in the second stage of Hamilton (1981) are more complex. It comprises the evolution of a hypognathous mouthcone including the tapering of the labium and labrum, the reduction of the size of the maxillary and labial palps, and the transformation of the mandible and lacinia into slender stylets with an internalized articulation (Hamilton 1981). Further sclerotized modifications occuring in this stage are the development of simple mandibular and maxillary levers, and wing-like invaginations of the hypopharyngeal fulturae (Hamilton 1981). Heming (1980) based on embryological data was one of the first who gave an idea of the mouthpart structure of an acercarian progenitor. Therefore, “typical biting and chewing mouthparts” were present with the galea fused to the stipes and a tendency of the

laciniae to invaginate and elongate (Heming 1980). These features are maintained in Psocoptera and Amblycera, however, showing a derived hypopharyngeal structure (Heming 1980). Yoshizawa & Saigusa (2003) showed that the galea and stipes are separated in Psocoptera. As a consequence, the latter proposed to consider the fusion of the galea and stipes, if at all, as synapomorphy of Thysanoptera and Hemiptera. The modification of the laciniae as already present in Psocoptera was likely a key innovation in the evolution of piercing and sucking mouthparts in Acercaria (Yoshizawa & Saigusa 2003). This concerns in particular its elongation and loosing thickness as preadaptation for piercing in Hemiptera and Thysanoptera. One can argue if the bi- to tri-furcated lacinial tip developed to the hemipteran maxillary rupturing devices (e.g. Brozek 2013b). Yoshizawa & Saigusa (2003) also considered the splitting and partly elongation of a single partition of the stipito-lacinial muscle (0mx6) of Psocoptera as a key innovation. This enables on the one hand more complex three-dimensional movements of the laciniae, and on the other a more powerful protraction which is essential for deep a penetration into the host tissue (Yoshizawa & Saigusa 2003). This is at least confirmed for Thysanoptera (e.g. Mickoleit 1963) and Sternorrhyncha (Weber 1928, 1929a, 1935). The evolution of the laciniae to long and slender stylets is fairly well comprehensible as the orthopteroid lacinia is already oblong (e.g. Matsuda 1965). Furthermore, no basic modifications of the musculature are required during evolutionary elongation.

The evolution of the mandible is far from being settled. The comparison of mandibular retractors and protractors of Hemiptera with adductors and abductors in Psocodea is apparently the main issue of muscular homologization (with respect to the labial musculature of the hemipteran rostrum). Snodgrass (1938) homologized his first mandibular retractor (1mdr, origin on vertex, insertion mesally on the base) with the orthopteroid mandibular adductor (M12a of Spangenberg et al. 2013b; 21 of Matsuda 1965; 0md1/M. craniomandibularis internus of Wipfler et al. 2011). This is supported by the distinct mandibular tendon functioning as attachment side, which is apparently always present mesally in Psocodea and posteriorly in Hemiptera (e.g. *Systelloderes*, Enicocephalomorpha, Heteroptera, Spangenberg et al. 2013b). The second mandibular retractor of Snodgrass (1938) (2mdr, originates on the gena, inserts laterally on the base) was homologized with the “primitive cranial abductor” (M12 of Spangenberg et al. 2013a,b; 23 of Matsuda; 0md3/ M. craniomandibularis externus posterior of Wipfler et al. 2013). However, the homology of the second mandibular retractor of Snodgrass (1938) with both muscle (22) of Matsuda (1965) and 0md2/M. craniomandibularis externus anterior of Wipfler et al. (2011) (present e.g. in *Liposcelis*) cannot apparently excluded. Matsuda (1965) also argued that the second mandibular retractor arising from the head capsule of Heteroptera (M12 of Spangenberg et al. 2013b) is likely also homologous to the tentorio-mandibular muscle (25, see below), assuming “that their origin from the cranial wall […] is a result of loss of the tentorial structures”. It is widely accepted

that the mandibular retractor originating on the anterior tentorial arm is homologous to the orthopteroid tentorio-mandibular muscle (see M12c of corrected fig. 11A of Spangenberg et al. 2013a; 25 of Matsuda 1965; 0md6/M. tentoriomandibularis lateralis inferior). However, at least in Tubulifera (Thysanoptera) (12. M. tentorio-labralis, Mickoleit 1963) and *Cerobasis* (Trogiomorpha) there is a second muscle originating on the anterior tentorial arm and inserting on the anterior edge of the mandibular base. This is also possibly homologous with 0md6. The mandibular retractor arising from the hypopharynx in hemipterans is only present in Enicocephalomorpha and Gerromorpha (M12b in Spangenberg et al. 2013b). Its homology with the hypopharyngo-mandibular muscle (26 of Matsuda 1965; 0md4/M. hypopharyngomandibularis of Wipfler et al. 2011) cannot be excluded. However, a shift of the origin to the hypopharyngeal wing in Heteroptera could be a consequence of the loss of the tentorium. It is apparently more parsimonious to accept the absence of the hypopharyngo-mandibular muscle in the proto-hemipteran instead of assuming multiple independent losses or that this muscle has re-evolved twice in the remaining subgroups. Sternorrhyncha, Auchenorrhyncha and Coleorrhyncha share the entire set of tentorio-mandibular muscles with each other but the hypopharyngo-mandibular muscle is consistently lacking (e.g. Weber 1928; Singh 1971; Spangenberg et al. 2013a).

That all generalized mandibular muscles are involved in retraction raises the question of the origin of the protractors. The tergal abductor muscle reversed its position to about 180° according to (Pesson 1944), an interpretation rejected by Heming (1980). Matsuda (1965) suggested that the lateral fronto-labral muscle (61 of Matsuda 1965; 0lb2/M. frontoepipharyngalis of Wipfler et al. 2011) was transformed into a mandibular protractor as it is presumably the case in Thysanoptera (M. clypeo-labralis lateralis of Mickoleit 1963; Moritz 1982b). Parsons (1974) considered the possibility that both heteropteran mandibular protractors “are new developments in Hemiptera and have no counterparts in orthopteroid insects”, an interpretation which is in contrast to a statement of Evans (1973): “it should never be assumed that any structure represented an entirely new development and could not have been derived from a preceding one”. Irrespective the muscular evolution of the mandible there is the question how an intermediate state between a generalized flattened biting mandible and an elongated one adapted only to piercing can be functional (see Parsons 1964: “It is difficult to explain how a hypopthetical stage-1 hemipteran could feed […]”)? One can speculate that the progenitor with a stylet-like mandible applied a similar feeding mechanism like recent Thysanoptera. As mentioned above a true mandibular protractor is absent in this taxon and piercing is only achieved by nodding the head (see also 4.3.2). It appears likely that incisivi (and likely molar teeth) of a generalized mandible developed to the barbed mandibular apex of the hemipteran stylet (e.g. Faucheux 1975; Cobben 1978; Brozek 2013b). The hypothetical stage two is the “temporarily end of the thysanopteran evolution” (Hamilton

1981). Staniczek (2001) added that the evolution of the dicondylic mandible is accompanied by the loss of the capability of protraction and retraction of the mandible, which also affect the specific musculature.

An evolutionary step which is not unequivocally assigned either to stage two or three of Hamilton (1981) is the evolution of the mandibular and maxillary plates. In general, the mandibular plate (lorum, juga) is located laterad to the clypeus and represents the sclerotized exoskeletal element of the loral lobe which serves as origin for the mandibular protractor muscles. The lorum could be either part of the mandible, the clypeus, the hypopharynx or the gena (summarized in Snodgrass 1938, Singh 1971 and Parsons 1974). Early embryological data of *Siphanta acuta* (WALKER, 1851) (Flatidae, Fulgoromorpha, Auchenorrhyncha) confirmed that the mandibular plates are not derived from the mandible which provides an argument for a parietal origin (Muir & Kershaw 1912). The mandibular plate of *Oncopeltus fasciatus* (DALLAS, 1852) (Pentatomomorpha, Heteroptera) is ontogenetically of dual origin derived not from the mandible, but partly from the surface of the head capsule (parietal) and from the lateral walls of the hypopharyngeal food pump (appendicular) (Newcomer 1948). The hypothesis of a clypeal origin is supported by Spooner (1938), Evans (1937, fossil evidence in 1957), and Kramer (1950) as in some members of Hemiptera (e.g. Coleorrhyncha and Fulgoromorpha) the proximal end of the plate is fused with the postclypeus. Consequently, the mandibular protractors would be of clypeal origin. An argument against the clypeal theory is the development of the functional mouth which would be inconsistent with that in other pterygote insects (Parsons 1974). I follow here the definition of Parsons (1974) stating “The functional mouth is the opening into the prepharynx, while the morphological mouth, marked by the frontal ganglion, leads into the pharynx”. The concept of Snodgrass (1938) favors the mandibular plate descending from the hypopharynx which in turn is derived from the mandibular somite. On the one hand the lora are partly fused with the hypopharynx mesally, and on the other the protractors of the mandibular stylet would be homologous to the hypopharyngeal muscle of the mandible in a generalized insect (Snodgrass 1938). The hypopharyngeal theory is supported by Butt (1943) and Parsons (1974). The latter described more reliable innervations of the mandibular protractors from the subesophageal ganglion rather than from the tritocerebrum. Parsons (1974) referring to Newcomer (1948) stated the absence of convincing embryological data, but she was obviously not aware the study of Singh (1971). The latter documented the embryological development of *Oxyrhachis tarandus* (FABRICIUS, 1798) (Membracidae, Cicadomorpha, Auchenorrhycnha). Therefore, the mandibular plate is first recognizable in the six day old embryo. It is formed by internal differentiation of the mandibular appendage into the mandibular stylet and the mandibular plate. Consequently, the lorum would be of mandibular origin. The connection of the mandibular plate with the hypopharyngeal wall in a ten days old embryo and more distinctly in the 14 days old

one would then be a secondary development (Singh 1971). The genal-subgenal theory with their followers is summarized in Parsons (1974). It is rejected by the latter as the scenario for the development of the mandibular plate is too complex in comparison with the hypopharyngeal one, it does not explain how the two-layered loral lobe arise from a single-layered gena, and finally the innervations do not fit together.

The following paragraph gains further knowledge about the appendicular concept (maxillary and mandibular plates arise from the maxillary and mandibular anlagen, maxillary plates homologous to stipes; Evans 1973) and parietal concept (maxillary and mandibular plates arise from the head capsule; Parsons 1964, 1974) others than in Spangenberg et al. (2013a, b). Somewhere in between of both theories is Duporte (1962) who argued that the maxillary plate is due to the fusion of cardo and stipes, and that both latter in turn are fused with the genae and postgenae. One of the earliest embryological studies to elucidate the origin of the maxillary plates was made by Muir & Kershaw (1912). They assumed a similar ontogeny for the mouthparts of Heteroptera, Cicadomorpha and Fulgoromorpha. Therefore, the maxilla arises from the distal portion of an undivided protuberance (“first maxilla”), and the maxillary plate from its proximal one. Muir & Kershaw (1912) supposed that the proximal portion represents cardo and stipes, and the distal one lacinia and galea. As a consequence, the maxillary plate is stipital in origin favoring the appendicular concept. Newcomer (1948) analyzed the embryonic development of the mouthparts in Heteroptera in the case of *Oncopeltus* (Lygaeidae, Pentatomomorpha). Therefore, and as in Auchenorrhyncha the maxillary plate originates as appendage from the proximal region of the pre-maxilla rather than from the head capsule. Parsons (1964) instead stated that the „maxillary and mandibular appendage anlagen produced only the stylets, and did not contribute to the head capsule.” Newcomer (1948) likewise builds a clear picture of the advanced stage in the development of the feeding stylet. Thus, the longitudinal growth is achieved by a proximal elongation. This induces the sinking of the mandibular and maxillary stylets into the head capsule during blastokinesis. The bristle pouches, one for each stylet, are formed during this process. The mandibular and maxillary sacs are ectodermal invaginations (Newcomer 1948). Bourgoin (1986a) gave a summary of the parietal and appendicular concept trying to explain the origin of the maxillary plates in Hemiptera. Apparently, he was not aware of the study of Leggett (1985) (as early personal communication in Heming [1980]), which was also overlooked by the present author in Spangenberg et al. (2013a,b). Leggett (1985) analyzed the mouthpart development in embryos of *Macrosteles* (Cicadellidae, Cicadomorpha) and documented the ontogenetic division of the maxillary appendage into a lacinial lobe on the one hand, and into a stipital lobe on the other. The lacinial lobe develops to the stylet-secreting organ whereas the stipital lobe gives rise to the maxillary plate! A similar scenario was just described for Auchenorrhyncha (Muir & Kershaw 1912; Singh 1971), Heteroptera

(Newcomer 1948) and Thysanoptera (Heming 1980). These are very strong arguments supporting the appendicular concept. According to the latter, the stipes bearing the maxillary palp finds its homologous organ in the maxillary plate bearing the Evans' organ (Evans 1973). Comparing the maxillary musculature of Hemiptera with more generalized insects (Psocodea, see above) gives an additional hint for the stipital origin of the maxillary plate. Thus, all lacinial protractors originate on the stipes (Fig. 5) which is similar in position to the maxillary plate, and none of them on genal areas as supposed in the case of the parietal concept. Consequently, the maxillary plate is considered as homologous to the stipes in the present study.

The third evolutionary step leading towards the hemipteran cephalic configuration includes the development of the tube-shaped labial rostrum, the complete loss of labial and maxillary palps (but see presumable homology of Evans' organ), the development of the sucking pump, further tapering of the labrum and final forming of the stylet levers (Hamilton 1981). Matsuda (1965) started the homologization of the hemipteran tube-like labium by counting from the prementum. Therefore, the latter is homologous to the basal labial segment. However, Matsuda (1965) also considered the proximal labial segment of Heteroptera to be "a segment secondarily acquired". As outlined above the three-segmented hemipteran labium is due to reduction of the first labial segment (e.g. Weirauch 2008). The gula of Heteroptera is no part of the labium (e.g. Seifert 2005). In the light of the above assumed homology, Matsuda (1965) homologized the hemipteran retractor or depressor of the labium (M17 of Spangenberg et al. 2013a,b) inserting either on the base of the first ("Homoptera") or second segment (Heteroptera) with the tentorio-premental muscle (34 or 35 of Matsuda 1965; 0la4 or 0la5 of Wipfler et al. 2011) or the postmento-premental muscle (38 of Matsuda 1965; 0la8 of Wipfler et al. 2011). According to Matsuda (1965) the protractor of the labium in Hemiptera (inserts on the unpaired apodeme of the second segment) is likely homologous to M. protractor hypopharyngis (25 of Mickoleit 1963; 79 of Matsuda 1965; 0hyx1). However, the origin of the former is variable and can also be on the second labial segment (e.g. Spangenberg et al. 2013b). Matsuda (1965) hypothesized that the prementum is not distinguishable in Hemiptera and either fused with the sclerotized ventral wall of the head capsule in Heteroptera or with the ventral neck region of "Homoptera". In the following Matsuda (1965) gave birth to a bold theory that the two to three segments distad to the prementum are modified and fused labial palps. This theory is based on the palpal origin of the rostrum in Siphonaptera and Diptera, and on the assumption that the intrinsic musculature of the labial palps of a generalized insect is the progenitor of the same in the tube-like distal labial segments. The embryological development of *Oxyrhachis* (Auchenorrhycha) documented by Singh (1971) showed two labial appendages lying close to each other in the six day old embryo and getting fused along theirs mesal sides in the nine days old embryo fitting in

Matsuda's (1965) scenario. However, this is apparently the way of development in all insects and there is no subsequent differentiation into labial palps, glossae or paraglossa (e.g. Goss 1953; Singh 1971). There a two other arguments against this theory. First, there is a general trend in Acercaria to reduce the labial palp (e.g. Psocomorpha, Badonnel 1934) and second its intrinsic musculature (e.g. Thysanoptera, Mickoleit 1963). Evolutionary speaking it appears unlikely that just the highly specialized and derived Hemiptera have maintained such primitive labial characters. Especially the intrinsic labial musculature of *Aphis* (Aphididae, Sternorrhyncha) (Weber 1928) is well-developed and hardly to homologize with the simple depressor and levator muscles of the single generalized labial segments. Crampton (1921) in Snoddgrass (1927) also "regards the basal segment of the cicada labium as the mentum, the next segment as the palpigers, and the third as the fused palpi. It is evident that the muscles of the labium […] furnish no clue to homologies with biting insects."

In an alternative concept the basal hemipteran labial segment was homologized with the postmentum, the second one with the prementum, and the two distal ones with "two apical endite lobes" (e.g. Pesson 1944; Poisson 1951). One can develop this thought further by assuming that the basal hemipteran segment is the submentum, the second one the mentum, the third one the prementum and the glossae and paraglossae are fused to form the apical segment. This theory is supported by the division of the postmentum in the basal Psocomorpha (e.g. Badonnel 1934; Cope 1940). Interestingly, Hamilton (1931, text-figure 1) documented for *Nepa* (Nepomorpha, Heteroptera) a pair of distinct lobed labial appendages originating on the base of the presumable third labial segment. Hamilton (1931) interpreted these appendages as true labial palps which would fit with their generalized origin on the prementum. Alternatively, one could speculate if these labial appendages are an atavism of true labial palps and, thus, also indicate the nature of the third labial segment as prementum. However, Hamilton (1931) did not mention the number of examined specimens. These new insights may also throw new light on the possible homology of the labial intercalary sclerites between the third and fourth labial segments with the labial palps. Intercalary labial sclerites between the first and second segment of Heteroptera are then a secondary development. Following the homology of the entire labial rostrum with the entire generalized labium one can speculate to the muscular homology of *Aphis* (Weber 1928) and *Stenopsoccus* (Badonnel 1934) based primarily on similar relative positions. The following homology-pairs are conceivable (hitherto not included in cladistic analysis) (Tab. 4):

Table 4: alternative homologization of the labial hemipteran muscualture

Aphis (Weber 1928)	*Stenopsoccus* (Badonnel 1934)	*Aeolothrips* (Mickoleit 1963)	Wipfler et al. 2011	Spangenberg et al. 2013a,b
m. abd3/m. abductor tertius labii	i, fléchisseurs internes de la glossa (prement-um->base of glossa)	20, M. retractor glossa (base of postmetum -> apodem of glossa)	0la12/M. praemento-glossalis	M22
m. trans5/m. transver-salis quintus labii	j, fléchisseurs lateraux de la glossa (lateral prementum near palpi-fer->medio base of glossa, near salivary orifice)	23, M.praementosalivaris anterior (base of prementum -> medial glossa)	0hy8/M. praemento-salivaris posterior	M21
m.trans 2 – 4/m. trans-versalis secundus – quartus labii	l, l, fléchisseurs externes (prementum -> outer base of 1st labial palpomere)	21, M.flexor palpi labialis (laterodistal prementum ->lateral base of 1st palpomer)	0la14/M. praemento-palpalis externus	M20a
m. add5/m. adductor quintus labii	k, muscles mentaux-lateraux transverses (postmentum near palpifer -> salivarium)	24, M.praementosalivaris posterior (proximal edge of prementum->near salivarium, but also from distal side of prementum to proximal)	0hy7/M. praemento-salivaris anterior	/
m.add4/ m. adductor quartus labii	p, muscles sternomentaux proximaux (lateral postentum -> medial base of prementum)?	/	0la8/M. submento-praementalis?	M20?
m.add3/ m. adductor tertius labii	p, muscles sternomentaux proximaux (lateral postentum -> medial base of prementum)	/	0la8/M. submento-praementalis	M20

m. trans1/m. transversalis primus pharyngis	/	/	/	/
m.add1/m. adductor primus labii	/	19.a M.retractor praementi lateralis (Kehlsporn->base of prementum)	0la4/M. postocci-pitpopraementalis	M17a
m.add2/m. adductor secundus labii	/	19.b M.retractor praementi lateralis cervical membrane>base prementum)	0la4/ M. postocci-pitpopraementalis	M18
m.abd1/m.abductor primus labii	/	/	/	M17
m.abd2/ m.abductor secundus labii	/	/	/	M19

One has to consider also that the development of the tube-like labium removes the tip of the labium away from the head capsule whereas the glossa and paraglossa in a generalized insect form its ventral closure. This different spatial distribution in Hemiptera can induce shifts of muscular origin. A drawback of the homology presented in this paragraph is that it does not explain the homology of the extrinsic labial and promoter muscles (see Matsuda 1965). Matsuda (1965) rejected this homology concept as it is “based primarily on a theoretical consideration that the four-segmented labium should a priori be comparable with four major parts of the generalized labium.” However, Matsuda (1965) also could only speculate about the supposed palpal origin. Neither of the both theories is, however, able to explain the homology of the crumenal musculature of Sternorrhnycha (muscle 21 and 22 of Singh 1971).

Embryological data is not sufficient to reconstruct the evolution of the hemipteran labium. Newcomer (1948) just reported for the 4.5 day old embryo of *Oncopeltus* a pre-labium with a basal segment and a non-segmented distal portion. Two days later the distal part is subdivided by two sutures forming the second, third and fourth labial segments (Newcomer 1948).

The presence of levers of the feeding stylets is apparently an autapomorphy of the hemipteroid assemblage. These sclerotized structures are responsible for indirect protraction or retraction of the stylets or act as a spacer between them and the head capsule. Both mandibular and maxillary levers of Hemiptera are secondary formations of the respective stylet pouch. The mandibular and maxillary sacs are invaginations of the head capsule im-

plying that both stylet levers are parietal in origin (Parsons 1964). Heming (1980) postulated the independent development of the levers from the stylets in Thysanoptera. Therefore, the appropriate lever has a different embryological origin, is not attributed to the stylet-secreting organ but to the bristle pouch, and develops “much later” than the stylet. According to Heming (1980) this delay is necessary as the lever can only be linked with a mature stylet in its final spatial configuration. In a further stage of the embryological development of *Haplothrips verbasci* the mandibular lever gets fused with the mandibular base to a single structure (Heming 1978, 1980). The homology and presence of the thysanopteran mandibular lever is doubtful, especially as it is not explicitly mentioned in the studies of Risler (1957), Mickoleit (1963), and Matsuda (1965). The principal problem is if the bristle pouches as origin of the levers derive from the mandibular or maxillary appendage, respectively, from other head appendages or from the external cuticle (Heming 1980). Following this argumentation the mandibular lever of Thysanoptera is in fact labral in origin as the mandibular sac for its part is formed by the lateral wall of the labrum and the medial wall of the left stipes (Heming 1980). This is contrast to the classification of the mandibular sac in Heteroptera (see below Newcomer 1948). The formation of the maxillary sac in thrips is much more difficult. It is build by the lateral walls of the labrum, the hypopharynx, the medial wall of the stipes and the anterior wall of the labium. However, the origin of the lever is apparently just restricted to the stipital part, hence, it is also stipital in origin (Heming 1980). The development of the stylets prior to that of the levers is also documented for Membracidae (Cicadomorpha, Auchenorrhyncha) (Singh 1971) and Lygaeidae (Pentatomomorpha, Heteroptera) (Newcomer 1948). According to the latter, the mandibular lever is a direct derivative of the mandibular sac, whereas the maxillary lever is segregated indirectly by a diverticulum of the maxillary sac.

The evolution of the tentorium has attracted little attention (e.g. Parsons 1964; Matsuda 1965). Puchkova (1970) supported the parietal concept and outlined the modifications of the hemipteroid head. She suggested that the “loss of the gnawing function of the mandibles led to reduction of the tentorium”. The argument fits with the condition in Heteroptera, but not with the presence of a well developed tentorium in members of Coleorrhyncha (Spangenberg et al. 2013a), Sternorrhyncha (Weber 1928, 1929a,b, 1935), and Auchenorrhyncha (e.g. *Philaenus* equipped with anterior, dorsal, and posterior tentorial arms). A potential synapomorhy of Condylognatha (Grimaldi & Engel 2005) is the dorsal shift of the anterior tentorial pits. However, this character state is not consistently present in the species under consideration here (e.g *Hackeriella*) and is therefore doubtful.

The hypopharynx of orthopteroid insects is a tongue-like structure and facilitates the transport of food particles whereas in Hemiptera it is not directly involved in the food uptake but in pumping saliva. The morphological transformations comprise the reduction of the oral, loral, and posterior hypopharyngeal arms, the extension of the suspensorial sclerites

(hypopharyngeal wings) and the reduction of the hypopharyngeal musculature (e.g. Matsuda 1965). According to Snodgrass (1938) the apical protrusion of the hypopharynx of some "Homoptera" is homologous to the generalized lingua. However, the presence of the membranous lingua is considered as ambiguous character as it is likely fused with the hypopharynx or not distinguishable. Snodgrass (1938) homologized the sitophore (present in Psocodea and orthopteroid insects) with the sclerotized pumping chamber of Hemiptera. Both structures represent a concave depression of the hypopharynx. In Hemiptera, however, it includes a membranous chamber and acts as salivary pump (for summary see Spangenberg et al. 2013a) whereas the function in Psocodea is not fully understood. The sitophore is either part of a "mortar and pestle" apparatus (e.g. Snodgrass 1944; Matsuda 1965) and/or involved in the excretion of saliva (von Kéler 1966b), but then less specialized as in Hemiptera. Assuming the homology of the complex psocodean hypoharyngeal mortar and epipharyngeal pestle apparatus with the complex hemipteran salivary pumping chamber including the piston (homology criterion of specific quality of Remane 1952) would imply that the latter is of epipharyngeal rather than hypopharyngeal origin. However, embryological data supporting this are not available (Newcomer 1948, Singh 1971; Matolin 1973). Furthermore, the pestle of Psocodea is directly linked with the epipharynx in adults (Rudolph 1982), whereas it is an independent structure distant from the epipharynx in Hemiptera (e.g. Spangenberg et al. 2013a,b).

Matsuda (1965) interpreted the sclerotized ring of the salivarium of Thysanoptera as a progenitor of a true salivary pump. The only well-developed hypopharyngeal muscle retained in Hemiptera (except the labial depressor discussed above) is the dorsal dilatator of the salivarium (71 of Matsuda 1965; 0hy12 of Wipfler et al. 2011; M23 of Spangenberg et al. 2013a,b). In Hemiptera the retractor of the piston of the salivary pump generally originates on the hypopharyngeal wings. Spangenberg et al. (2013b) stated that the origin on the postoccipital region in *Systelloderes* (Enicocephalomorpha) and *Hydrometra* (Gerromorpha) is likely due to the extreme elongated condition of the head capsule. However, Butt (1943) reported that the piston retractors of *Oncopeltus* (Pentatomomorpha) also originate on the head capsule which is not extremely elongated in this case. In Hemiptera this muscle is attached to the salivary piston (Spangenberg et al. 2013a) and in Thysanoptera to a homologous membranous portion (Mickoleit 1963). Matsuda (1965) interpreted the thysanopteran salivarium with its sclerotized ring as precursor of a membranous piston and at least one valve as a precursor of a specialized salivary syringe as it is present in Hemiptera. This is confirmed in the present study. The pestle of Psocodea, however, is moved by a clypeal muscle (82 of Matsuda 1965; 0bu1 of Wipfler et al. 2011). The salivaria of Coleorrhyncha

and Sternorrhyncha are equipped with more than one hypopharyngeal muscle (e.g. Weber 1928; Spangenberg et al. 2013a). I accept the view of Matsuda (1965) that “Plural numbers of this muscle in the sternorrhynchous Homoptera have been derived by a secondary split of originally one muscle”. However, the clearly different hypopharyngeal attachment sites of m.dil.cup3+4 of *Aphis* (Weber 1928) reject the split of an originally single muscle.

4.3 Feeding habits in Hemiptera and Thysanoptera (Condylognatha)

4.3.1 General remarks and diversification of phytophagous groups

The vast majority of hemipteran species, especially in the traditional “Homoptera” (Sternorrhyncha and Auchenorrhyncha), are obligatory plant feeders, and very often specialized on xylem or phloem vessels (e.g. Miles 1968; Backus 1988; Schaefer & Panizzi 2000; Strümpel 2005a). It is conceivable that sucking nutrient rich fluids from the vascular system is more efficient than feeding on plant substrates with biting orthopteroid mouthparts as it is for instance the case in Phasmatodea (Blüthgen et al. 2006; Friedemann et al. 2012). Hemipterans comprise almost 100.000 described species and are the largest subgroup of Acercaria (Deckert & Göllner-Scheiding 2005; Strümpel 2005a,b,c). This tremendous diversity is likely correlated with the radiation of seed plants at the Carboniferous-Permian boundary and with the late cretaceous radiation of angiosperms (Misof et al. subm.) (sequential evolution, Jermy 1984). For comparison, the diversification of Phthiraptera and animal affine Liposcelididae correlated with the radiation of birds and mammals at the Cretaceous-Paleogene boundary (Grimaldi & Engel 2006; Misof et al. subm.). The biodiversity among birds (ca. 10.500 species) (Gill & Donsker 2014) and mammals (ca. 5.400) (Wilson & Reeder 2005) is lower by a factor of about 18 than the diversity of seed plants (ca. 300.000) (http://www.flora.dempstercountry.org/0.division.pages/Spermatophyta.html, accessed on 01.09.2014). This in combination with the shorter period of time is likely the reason for the lower diversity of lice and Liposcelididae lineages, respectively (see also Mey 2005). These considerations are conform with the “adaptive-zone hypothesis”, which predicts “that if multiple lineages have invaded a new adaptive zone, they should be consistently more diverse than their (equally old) sister groups, when the latter retain the more primitive way of life” or more in detail “that the origination of phytophagy (like other novel ways of life) should speed diversification with respect to sister lineages retaining more-primitive habits, because it results in a kind of ecological release” (Mittler et al. 1988). The switch from detrivory (e.g. Psocoptera) to phytophagy is impeded by three evolutionary barriers (Southwood 1973). One problematic factor is the risk of desiccation during the exposed feeding on plants. Another

challenge is to attach to and to walk efficiently on the host's surface, which is often impeded by defensive mechanism such as layers of wax or hairs (e.g. Beutel & Gorb 2001). The third challenge is to cope with the lower energy-efficiency of plant tissues compared to detritus or animal matter (Southwhood 1973). Mastering these barriers offered the insects a large biomass with a great variety of resources which apparently greatly stimulated the radiation of phytophagous insects (see Strong et al. 1984). One aspect of this diversification is the capacity to modify adhesive devices on the distal parts of the legs, which are essential for attachment and efficient locomotion (Friedemann et al. 2013). Within this framework phytophagy evolved within nine insect orders, presumably at least 50 times independently (Mittler et al. 1988).

The saps of the xylem and phloem represent substantial nutrient resources and can be absorbed almost without digestion (Raven 1983; Chapman RF 2003). The phloem is a tissue with a symplastic transport of nutrients. That implies the transport of calcium, sugars, amino acids and potassium through the cytoplasm of the single cells. In general the sieve tubes are characterized by a positive turgor (Raven 1983). In contrast, the transport in xylem of a transpiring plant is of apoplastic character. The solution of organic carbon and nitrogen is less concentrated than in the phloem resulting in low nutritional or energy value. It is transported through the diffusion site of the cell walls (Raven 1983). As the liquids in the xylem are poorer in nutrients, xylemomyzous species demand higher feeding rates than in those specialized on the phloem (Novotny & Wilson 1997). The turgor in the xylem is negative (e.g. up to -10 bar hydraulic tension in *Vicia faba* L. (Fabaceae) which is one host plant of *Philaenus spumarius* (Malone et al. 1999); see also the "Cohesion-Tension Theory").

4.3.2 Host finding and feeding habits in the subgroups

Specific host recognition is achieved by dabbing the labial tip on the plant surface (Auchenorrhyncha, Coleorrhyncha) or by probing bites (without producing a salivary sheath) with additional antennal contact (Psylloidea, Aphidoidea, and likely Heteroptera) (Backus 1988; Freeman et al. 2001). For exposing the feeding stylets the labium has to change its shape. In Heteroptera it bends distally between labial segments II and III, and proximally between labial segments I and II during feeding (see fig. 96 in Jordan 1972). In Auchenorrhyncha, Aphidoidea and Aleyrodoidea it is retracted into the head or prothorax with a simultaneous telescoping mechanism (Weber 1929b). The labium of Psylloidea is bent between segments I and II and is also retractable, whereas no externally visible modification of the labium occurs during sucking in Coccoidea (Weber 1929b). Different stylet movements in Heteroptera, Sternorrhyncha and Auchenorrhyncha are summarized in Backus (1988). In

the two former groups the complete stylet bundle enters the plant tissue, whereas in the latter the mandibles are anchored in the outer cell layers of the host, and the maxillary stylets as the main piercing organs penetrate deeper layers (see also Mora et al. 2001). In the latter case the maxillary stylets are longer than the mandibles and their apex is sharpened (Qadri 1949). Interestingly, the stomata are very rarely used as entrance into the internal plant tissue (Freeman et al. 2001). Tjallingii & Esch (1993) confirmed for Aphididae that stylet penetration is apparently only due to mechanical movements without support of cell-wall-decomposing pectinase. McAllan & Adams (1961) investigated a more extensive sampling of aphids and showed that some species produce pectinase. Thus, only the pectinase-producing species penetrate between the cells by decomposing the pectic middle lamella ("macerate and flush feeders" of Hori 2000). Aphids lacking pectinase penetrate through the plant cells directly taking the line of least resistance (McAllan & Adams 1961) and this is also the case in the majority of Aleyrodidae (Freeman et al. 2001). Cell wall-degrading enzymes, especially as compounds in the watery saliva, were documented for the xylem-feeding *Homalodisca vitripennis* (GERMAR, 1821) (Cicadellidae, Cicadomorpha) (Backus et al. 2006b) and for the omnivorous Miridae (Cimicomorpha) (see Boyd et al. 2002).

Auchenorrhyncha evolved three different types of phytophagous feeding habits, which can occur separately in specialized species or combined in a single one (e.g. Day et al. 1952; Backus 1985; Tavella & Arzone 1993). Obligatory xylem-feeding (xylemomyzous species) is apparently restricted to the cicadomorph Cercopoidea, Cicadoidea and Cicadellini, whereas phloem-feeding (phloemomyzous species, feeding on sieve-tubes) is likely characteristic for Fulgoroidea and Cicadelloidea except Cicadellini and Typhlocybinae (summarized in Novotny & Wilson 1997). Mesophyllomyzous (feeding on parenchyma and non-vascular tissue; "lacerate-and-flush" feeders in Backus 1988) and phloemomyzous species occur in Typhlocybinae (Cicadellidae) (Tavella & Arzone 1993). However, Day et al. (1952) and Naito (1977) reported for some phloem-feeding and mesophyll-feeding species of Cicadomorpha that they also occasionally suck xylem sap and vice versa. Phloem-feeding also occurs in Sternorrhyncha (Mittler 1957; Raven 1983; Backus 1988; Novotny & Wilson 1997).

Coleorrhyncha as non-vascular tissue feeders live on bryophytes (Goodchild 1966; Burckhardt 2010). In contrast to the tracheophytes, the bryophytes are characterized by a weakly developed cuticle and the absence of lignin (still controversial) both probably affecting the strength of the tissue (Glime 2007). The texture of the bryophytous plant is squamous or soft and true lignified tracheids or vessels are absent (Glime 2007). It is conceivable that the mandibular stylets are less stressed mechanically during piercing and ripping the plant, in comparison with their function in the more strengthened tissue of tracheophytes. This is likely the reason why the teeth on the saw-like mandibular tips of the bryophytophagous Coleorrhyncha are only feebly developed, compared to those of tracheophytophagous mem-

bers of Pentatomomorpha (e.g. Coreidae, Pentatomidae [Cobben, 1978]), which have to cope with lignified and thus strengthened cuticle and tracheids. However, there also tracheophytophagous groups of Hemiptera (e.g. Auchenorrhyncha [Strümpel 2010], Thaumstellidae and Berytinidae (Pentatomoprha) [Cobben 1978]) with a mandibular serration similar to that of Coleorrhyncha. A distinct correlation between the development of the mandibular teeth and the texture of the plant tissue is not verifiably. In this context it is noteworthy that the teeth of the mandibular tips of predaceous heteropteran species are strongly developed (e.g. Swart and Felgenhauer 2003). The mandibular musculature and the salivary complex do not show an apparent correlation with feeding on moss.

The highly diverse Heteroptera, the putative sister group of the relict group Coleorrhyncha, are highly versatile in their food preferences. They contain species feeding on all parts of spermatophyta (phytophagous), on animal tissue (carnivorous), or on both (omnivorous) (e.g. Cobben 1978; Schuh & Slater 1995; Boyd et al. 2002). It is conceivable that the ability to adapt to a broad spectrum of food substrates has contributed to the diversification. However, the species number in the strictly phytophagous Auchenorrhyncha is also very high.

The feeding modes of Thysanoptera are highly diverse in terms of the trophic level (predaceous, herbivorous, omnivorous), host tissues (leaves, pollen, animal tissue) and polyphagy versus monophagy (summarized in Brodbeck et al. 2002). It is assumed that ancestral thysanopterans were feeding on fungi or detritus (Mound & Heming 2000). Thrips pierce and suck single cells of plants, fungi or other arthropods (Mound & Morris 2007). Miles (1972) described this mode as “scratch-and-suck feeding” which is likely also the ancestral feeding habit of Condylognatha. Despite the broad spectrum of substrates the feeding stylets are uniform in structure throughout the subgroups (Mound & Heming 2000). However, it is difficult to determine the plant tissue (except flower-feeding species on pollen) or the exact nutritional portion which is ingested (Brodbeck et al. 2002). Thrips use a feeding mechanism similar to that of Hemiptera and their host exploration strategies are similar to those occurring in Sternorrhyncha and Heteroptera. A suitable host is identified by antennal movements towards the (plant) surface and by labial dabbing (i.a. paraglossal contact) (Hunter & Ullman 1992, 1994). In contrast to Hemiptera, host-identification is also supported by scraping movements of the pretarsal claws of the forelegs with subsequent wiping on the antennae (Hunter & Ullman 1989), and by scanning the surface using sensilla of the maxillary and labial palpi (Heming 1978). Piercing in Thysanoptera is characterized by a contraction of the mouthcone relative to the feeding stylets (Heming 1978). The single mandible is the main piercing organ penetrating a single cell or a group of adjacent cells (e.g. Heming 1978; Hunter & Ullman 1989). After piercing, the saliva is injected flowing through a canal formed by the glossae proximally and probably by the interlocked maxillae distally (see fig. 24 in

Hunter & Ullman 1992). However, there is no separation of the food and salivary canal between the connected maxillae (Hunter & Ullman 1992). Heming (1978) observed that salivation and ingestion do not occur simultaneously in larvae of *Haplothrips verbasci* (OSBORN, 1897) and concluded that the single canal composed of the interlocked maxillary stylets acts as salivary canal during secretion of saliva, and as food canal during uptake of food in the opposite direction. In contrast to Hemiptera, the specific function of the saliva (excluding the transfer of gustatory molecules) is less understood (Heming 1978). After successful probing by the maxillae (including gustatory evaluation by precibarial sensilla) the liquefied food is completely sucked up without involvement of a salivary sheath (e.g. Kloft & Erhardt 1959; Hunter & Ullman 1994). However, Moritz (2006) reported partly gelling saliva sealing the pierced cells and inhibiting uncontrolled leaking. The partly gelling saliva is possibly a preadaptation towards forming salivary sheaths (discussed below). In Thysanoptera the entire complex of the head and prothorax are pressed down for piercing (Hunter & Ullman 1989) as a true mandibular protractor is missing (Risler 1957; Mickoleit 1961; Mickoleit 1963). Schliephake & Klimt (1979) compared the movement of the head during piercing with the knocking of a woodpecker.

4.3.3 Salivary sheath

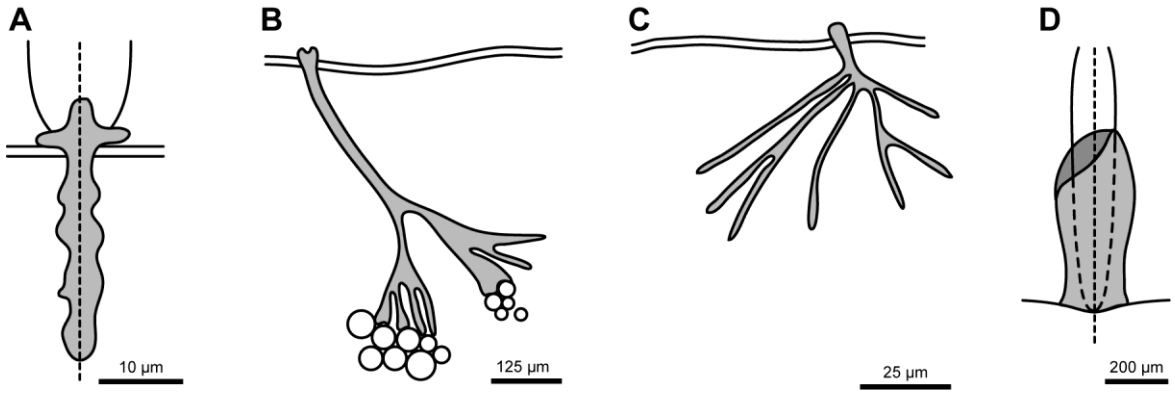

Figure 30. Schematic overview of some salivary sheaths (grey) formed by Hemiptera, narrow dotted line indicates feeding stylets. A: external and internal unbranched sheath of *Acyrthosiphon pisum* HARRIS, 1776 (Aphidoidea) feeding on an artificial diet (Miles 1972, modified); B: external and internal branched sheath of *Homalodisca coagulata* (SAY, 1832) (Cicadomorpha) feeding on xylem-vessels (Leopold et al. 2003, modified); C: external and internal branched sheath of *Bemisia argentifolii* BELLOWS & PERRING, 1994 (Aleyrodoidea) feeding on phloem (Freeman et al. 2001, modified) (see also Weber [1930] for Coccoidea); D: external unbranched sheath of *Dysdercus koenigii* (*Fabricius,* 1775) (Heteroptera) feeding on a cotton seed (Saxena 1963, modified).

Salivary sheaths (or stylet sheaths) enclosing the stylets within the biting canal are largely restricted to xylem- and phloem-feeders (summarized in Backus 1988). They only occur in Pentatomomorpha, some members of Cimicomorpha (see below), Auchenorrhyncha

and Sternorrhyncha (e.g. Cobben 1978; Miles 1968; Press and Whittaker, 1993; Freeman et al. 2001). According to Miles (1968, personal communication MH Sweet) carnivorous species of Pentatomidae and Lygaeidae (Pentatomomorpha) also form salivary sheaths. This observation is also confirmed for some species of Nabidae and Reduviidae (Friend & Smith 1971; Cohen 1990). The capacity to form salivary sheaths is arguably a ground plan feature of Hemiptera (Miles 1972), but it is presently unclear whether this applies to Coleorrhyncha and potentially basal groups of Heteroptera (e.g. Enicocephalomorpha, Dipsocoromorpha). The production of a salivary sheath in *Dysdercus* (Pyrrhocoridae, Pentatomomorpha) was documented in detail by Saxena (1963). The sheath is formed by viscous acidic saliva (pH 5.2 – 6.0) which forms a stout hyaline tube when it solidifies. It is extremely resistant against water and organic solvents. The sheath material is composed of a liquid "precursor" that is secreted by the anterior lobe of the principal salivary gland, lipoproteins, non-gelling proteins, free amino acids such as tyrosine and dihydroxyphenylalanine, and phenolase, which is produced in the accessory salivary gland (Miles 1964, 1972) (in "Homoptera" phenolase is secreted by cells of the principal gland, see Miles 1968). Another function of the accessory gland is the secretion of diluted saliva which facilitates the contact between the host plant and the gustatory sensilla of the stylets (Miles 1972). Components of the watery saliva are secreted by the posterior lobe of the principal gland. The gelling of the sheath-forming saliva is achieved by the oxidation of the precursor (likely supported by phenolase) and subsequent disulphide-, hydrogen- and quinine-bonding (Miles 1972). The salivary sheath acts as a guiding device for the labium. In contrast to Sternorrhyncha and Auchenorrhyncha (see below), the salivary sheath of Heteroptera is grafted on the plant surface and does not enter the host tissue. An external salivary sheath ("salivary collar") of the carnivorous lygaeid species *Geocoris punctipes* (SAY, 1832) was secreted on an artificial food source and also grafted on the surface (Cohen 1990). *Dysdercus* species (Backus 1988) feed on a variety of host plant tissues and this can differ even between individuals. However, salivary sheaths are only formed in the case of non-ingestible, robust, and non-porous surfaces such as leaves covered by a strongly developed cuticula or seed capsules (e.g. Saxena 1963; Miles 1972). *Dysdercus* and *Oncopeltus* (Lygaeidae) share a collar-like sheath of coagulated saliva outside of the plant tissue, but the sheath of the latter is inserted into the mesophyll, xylem or phloem (Miles 1959). This in contrast to the results of Saxena (1963) who provided evidence by application of sheath-staining with bromocresol purple that there is no internal salivary sheath following the path of the stylets. The only way to solve this is by assuming different chemical compositions of the internal and external part. This topic is touched upon by Miles (1960a) as he documented variations in staining reactions in different sections of a single stylet pathway. Miles (1972) pointed out that a salivary sheath only composed of the external "flange" just occurs during seed-feeding. The salivary sheath is likely also responsible for

sealing the bite canal against the feeding stylets to prevent the escape of injected saliva and liquid or liquefied food (Miles 1972).

Day et al. (1952) were one of the first who documented the formation of stylet sheaths in auchenorrhynchous Jassidae (Membracoidea). Thus, there is in general a characteristic pattern of the sheaths in the single genera referring to termination in host tissue, curving, terminal branching, diameter and number. The formation of the sheath starts with the piercing of the feeding stylets and theirs partly withdrawal afterwards. Following the latter step a "small particle" is present at the tip of the stylets (Day et. al 1952). This particle is apparently a drop of non-watery saliva which is capable to solidifying (see above). The drop is moulded to the typical tubular sheath during the next forward movement of the stylet bundles. The sheath is prolongated by the breakthrough of the stylets on the tip to form a new partition. This process is repeated several times up till the plant vessel for food-uptake is reached and is likely characteristic for all Hemiptera (Day et al. 1952; Miles 1964, 1972). The salivary sheaths of Cicadellidae are facultativly branched, in general xylem-terminating and composed of an internal intracellulary portion and an external part situating on the epidermis (Leopold et al. 2003).

The mandibles and maxillae of *Tuberolachnus salignus* (GMELIN, 1790) (Aphididae, Sternorrhyncha) enter both intracellular and intercellular space on the path to the sieve tubes (Mittler 1957). As a consequence, the surface of the sheath is smooth within the cells and roughened between them. However, Mittler (1957) did not explain whether the different external appearance is generated by the aphid itself or if it is a defense reaction of the host plant or an artifact due to staining or sectioning (see Tjallingii & Esch 1993). The terminal branching of the salivary sheath in *Tuberolachnus* is facultatory. Mittler (1957, 1972) suggested that this structure is, on the one hand, a haustorial organ gathering phloem sap from the surrounding pierced cells, and on the other it allows the stylets to feed on more than one vessel without withdrawals and re-piercings. The chemical properties of the salivary sheaths and the origin of the salivary compounds are constant within Hemiptera (Miles 1965).

A prerequisite for forming a salivary sheath is apparently the capability of producing two different types of saliva (linked with the subdivision of the principal gland), an alkaline component that remains liquid and an acidic one for coagulating (Miles 1959, 1960b; Saxena 1963). The watery saliva may serve for leaching or extra-intestinal digestion of starch with subsequent resorption (Miles 1959). However, Miles (1972) argued that there is a high diversity of the composition of the watery saliva of phytohagous Hemiptera impeding to reconstruct their exact function. Tjallingii & Esch (1993) documented coagulated phloem proteins in the pathway of the stylets of aphids, which are likely involved in the formation of a salivary sheath. In general, the salivary sheath is formed by the insect during feeding on solid foods and not during ingestion of free liquids (Cohen 1990).

4.3.4 Ancestral feeding habit of Hemiptera – carnivory vs. phytophgagy

The ancestral feeding type in Hemiptera and especially in Heteroptera is discussed controversially. Miles (1972) listed five different hemipteran feeding modes: scratch-and-suck feeding, stylet-sheath feeding, lacerate-and-flush feeding, predation, and blood-sucking. Among extant hemipterans obligatory carnivory occurs only in the heteropteran subgroups Enicocephalomorpha, Dipsocoromorpha, Leptopodomorpha, Nepomorpha, and Gerromorpha (Cobben 1978; Schaefer 1997). Spitting viscous saliva with a toxic effect on arthropods used as defense mechanism additionally separates predaceous true bugs from blood-feeding species (Miles 1972). The diversity of predaceous species is higher than that of herbivores in Heteroptera (Schaefer 2003). Cimicomorpha and Pentatomomorpha display the broadest spectrum of feeding habits including phytophagy, omnivory, and carnivory (summarized in Eubanks et al. 2003). Omnivory has evolved several times within different heteropteran lineages (Eubanks et al. 2003). Polyphagy and feeding on solid plant organs such as seeds, arguably a preadaptation to omnivory, developed in terrestrial heteropteran groups, and this is possibly an additional reason for the evolutionary success of true bugs (Eubanks et al. 2003). Schlee (1969) was one of the first who summarized the two conflicting theories stating either a phytophagous or a carnivorous ancestor. In the following I take the view of Sweet (1979) that “It is, evolutionally speaking, easier to lose complex attributes than to gain them, and complex characters, once lost, are rarely re-gained in the same original form” (see also Gould 1970). According to Schlee (1969) the concept of a plant-feeding protoheteropteran is supported by the general phytophagy in the related groups Coleorrhyncha, Auchenorrhyncha, Sternorrhyncha, and partly in the putative sister group Thysanoptera. Schaefer (2000, 2003) documented phytophagous taxa only occasionally pierce animals as aberrant hosts. In the conflicting scenario of a carnivorous ancestor, phytophagy had to be evolved several times independently which is evolutionary speaking unlikely. The evolution of carnivorous lineages from phytophagous groups is apparently more frequent (e.g. Geocorinae, Asopinae (Pentatomomorpha)) then the opposite case (Sweet 1979). Additionally, there are no predators known in “Homoptera”. Schaefer (1997) argued that “Homoptera” (in contrast to Heteroptera) feeding on nitrogen-poor plant saps are highly adapted and that this prevents exploitation of an animal nourishment. This argument is also in agreement with Sweet (1979). Schlee (1969) concluded that the phytophagous feeding type was likely a character in the stem group of Psocodea + Thysanoptera + Hemiptera. A further argument supporting phytophagy is the presence of “a-symbiotes” in Heteroptera with mycetomes. Assuming that the “a-symbiosis” is a primary character of Hemiptera, then also Heteroptera are primarily phytophagous (Schlee 1969). Mycetomes for housing symbiotes are present also in “Homoptera” (Ammar 1985) and Coleorrhyncha (e.g. Larivière et al.

2011). The absence of such a symbiosis in the outgroups Thysanoptera and Psocoptera is apparently due to theirs non-vascular tissue feeding (Schlee 1969; Heming 1978). Symbiotes are presumably only essential in the case of feeding on poor nutritional plant saps (Schlee 1969).

Sweet (1979) favoring the herbivorous origin of Hemiptera discussed that the development of the salivary sheath within Hemiptera was a single event and occurred prior to the splitting in the single subgroups. This implicates the loss in all Heteropterans except single taxa of Pentatomomorpha and Cimicomorpha (see above) which is likely due to different feeding habits (Sweet 1979). Assuming a predaceous protohemipteran implies that the evolution of the salivary sheath had to be occurred several times independently within the groups of Hemiptera which is not the most parsimonious explanation. Sweet (1979) argued that the tube-like labium including the feeding stylets is primarily adapted to unidirectional piercing on plant tissues and not animal tissues. This becomes clear in comparison to other carnivorous insects (e.g. Odonata, Neuroptera, Coleoptera) which developed chewing mouthparts with plate-like mandibles and maxillae for lateral biting (Sweet 1979). Additionally, the needle-like mouthparts are able to stick through the external cell layers of the plant which are not digestible anyway (Goodchild 1966). According to Sweet (1979) the gula is an essential organ in the carnivorous feeding mechanism. It is absent in “Homoptera” denying a common predaceous ancestor. Protoheteropterans feed on plant tissues which are rich in nutrients such as fruits or apical meristems. This feeding mode apparently needs no specialized adaptation, but, the gula evolved in this way during the evolution of the prognathous head (Sweet 1979). The mouthparts which are directed forward are a preadaptation for searching and probing on first animal food such as eggs or inactive prey (Sweet 1979). In contrast, the hypopgnathous condition of the head and mouthparts in phloem- and xylem-feeding “Homoptera” facilitates a “downward drilling” of the feeding stylets in the strengthened tissue of the plant vessels (Sweet 1979).

Assuming a phytophagous protohemipteran and protoheteropteran as supposed by Schlee (1969) and Sweet (1979) imply that Pentatomomorpha are primarily phytophagous (see also Eubanks et al. 2003). Miridae and Tingidae, both lineages in the group of Cimicomorpha with a carnivorous ancestor (Eubanks et al. 2003), are characterized by secondary phytophagy “but in a carnivore-like manner, using a toxic saliva to destroy patches of cells” (Goodchild 1966; see also Miles 1972). The salivary sheath is absent in both families and could not re-evolve or, vice versa, accepting a herbivorous ancestor of Cimicomorpha, the sheath would be an early loss (Sweet 1979). On the other hand the scenario of a phytophagous protoheteropteran requires multiple independent renunciations of this feeding habit in Enicocephalomorpha, Dipsocoromorpha, Nepomorpha, Gerromorpha and Leptopodomorpha. This is not satisfying either.

Schlee (1969) mentioned only one doubtful argument speaking for a carnivorous protoheteropteran. He argued that the absence of the filter chamber in Heteroptera is a hint against primarily phytophagy. However, he likewise denied this conclusion as the filter chamber evolved several times convergently in “homopteran” groups. Of course it is also possible that the filter chamber was already present in the protohemipteran and then lost in the archaic Heteroptera (parsimony). Cobben (1968, 1978, 1979), Schaefer & Panizzi (2000), and Schaefer (1997, 2003) are the main proponents of the concept proposing a carnivorous protohemipteran and protoheteropteran. The hypothesis of Cobben (1978, 1979) is largely based on an archaic character of Gerromorpha including a basal phylogenetic position, “possibly with the exclusion of Dipsocoromorpha and Enicocephalomorpha” (Cobben 1979). However, considering current comprehensive morphological and molecular studies to heteropteran phylogeny (for summary see Spangenberg et al. 2013b) the basal gerromorph position is far from being settled. The maxillae of Gerromorpha are strongly barbed. According to Cobben (1978) this is a character which is not adapted primarily to phytophagy. Additional support of the carnivory concept is derived indirectly from the evolution of the egg-system (Cobben 1968), and by the archaic damp litter-zone habitat retained partly in Gerromorpha (Cobben 1979). Schaefer (1997) *believed* Heteroptera is primitively carnivorous as the majority of the basal subgroups are also carnivorous. Schaefer (1997) also argued that it is a major step in evolution from herbivory to carnivory, and that a renunciation from a nitrogen-rich diet in carnivorous lineages to a nitrogen-poor one in herbivorous taxa appears difficult.

Assuming a predaceous protoheteropteran requires only one re-evolvement of phytophagy in the ancestor of the sister-groups Pentatomomorpha and Cimicomorpha (see also Goodchild 1966), with secondary carnivory except in Miridae and Tingidae. Concluding, the truth lies probably somewhere in between of Cobben and Sweet. That means that the idea of a herbivorous ancestor of Hemiptera in general apparently requires the less evolutionary steps. The least changes concerning the feeding habits of Heteroptera are presumably achieved by assuming a carnivorous ancestor within phytophagous Hemiptera.

4.3.5 Adaptation of xylem-feeding and phloem-feeding

In general there are fewer and less sharp mandibular teeth in phytophagous Hemiptera than in carnivorous taxa. Furthermore, the lacinia of the former is usually glabrous without teeth or comb-like hairs (e.g. Faucheux 1975). However, there exists no distinct morphological adaptation of the length of the feeding stylets concerning the different phytophagous feeding habits and host tissues. The commonalities in the ratios between the length of the

mandibular and maxillary stylets are due to the same systematic status rather than nutritional purpose (Backus 1985; Tavella & Arzone 1993). Furthermore, the morphology and arrangement of the precibarial sensilla is constant throughout the different tissue-feeder (Backus & McLean 1983). On the other hand, there is likely a trend in xylemophagous species to develop a more powerful set of cibarial dilator muscles to compete with the negative turgor in the xylem-vessels (Backus 1985; Tavella & Arzone 1993; Novotny & Wilson 1997; Malone et al. 1999). Consequently, xylem-feeders have to actively overcome this high tension and spend more energy for sucking than phloem-feeders. In the latter, referring to the positive turgor, the sap is forced into the gut of the insect which is of more efficiency (Raven 1983). Following the assumption of Peters (1983) that "maximum work generated by a muscle contraction is directly proportional to muscle volume" shows the volume of the cibarial dilatators is an index of the capacity of the food pump (Novotny & Wilson 1997). The efficiency of the cibarium is linked with the structure of the postclypeus as appropriate muscle attachment side. It is bulge-shaped, ripped and distinctly enlarged in the xylem-feeding *Philaenus spumarius* (Mallone et al. 1999) and more flattened, smoothed and moderately enlarged in the phloem-feeding *Nilaparvata lugens (*Delphacidae, Fulgoromorpha) (O'Brien & Wilson 1985). The trend of a more powerful cibarium is supported indirectly by the linked excretory capacity. In the xylem-feeders *Philaenus spumarius* it is of 500 to 1000 mg mg^{-1} $24h^{-1}$ (Wiegert 1964; Horsfield 1977) or of 2500 ml $24h^{-1}$ in *Graphocephala atropunctata* (SIGNORET, 1854) (Cicadellidae, Cicadoidea) (Backus 1985) in comparison to the phloem-feeders *Tuberolachnus salignus* (GMELIN, 1790) (Lachnidae, Aphidoidea) with 10.6 mg mg^{-1} $24h^{-1}$ (Auclair 1963; Press & Whittaker 1993) or *Strophingia ericae* (CURTIS, 1835) (Aphalaridae, Psylloidea) with 2.4 mg mg^{-1} $24h^{-1}$ (Hodkinson 1973; Press & Whittaker 1993). The ingestion and resulting excretion rate in the mesophyllomyzous *Empoasca abrupt*a DELONG, 1931 (Cicadellidae) is "very tiny" (Backus 1985). Additionally, phloem-feeding species soak up a large amount of organic carbon compounds whereas nitrogen is in short supply. As a consequence, theirs excretions are rich on sugars while those of xylem-feeders are more diluted and voluminous (Raven 1983). Other potential characters of obligatory xylem-feeders are the heavily sclerotized dorsal region of the food pump with a prominent tendon where the cibarial dilatators are attached (especially in *Philaenus*); a robust and strengthened precibarium; a wide lumen of the cibarium and precibarium; widely space D-sensilla in contrast to narrowly-spaced D-sensilla in phloem-feeder; and inflexible and robust feeding stylets for mechanical ripping of strengthened xylem-vessels (Backus & McLean 1983; Backus 1985; Press & Whittaker 1993). Novotny & Wilson (1997) gave the theory that there is a trend to an increasing body size of xylem-feeders compared to phloem-feeders or that there is a limit in miniaturization in xylemomyzous Auchenorrhyncha. This is due to the facts that "small species have relatively high metabolic rates and small feeding apparatus" and

“the smaller the species, the higher the pressure that must be generated to overcome resistance of feeding apparatus” (Novotny & Wilson 1997). The larger body size and the larger volume of the clypeus in xylem-feeders are likely linked with the relative length of the proboscis and the diameter of the food-canal. However, comparisons of the ratios in phloem-feeding species are absent (see Novotny & Wilson 1997). In general, xylemomyzous cicadas feed on a wide host plant range which is an advantage in the case of poor nutritional plant saps (Novotny & Wilson 1997).

Hemiptera not feeding on xylem- or phloem-vessels apply the “lacerate and flush” feeding (Miles 1972). Cohen (1990) outlined this scenario in detail for carnivorous Heteroptera. Thus, the feeding stylets are capable to splaying independently and crushing the internal organs of the prey. Subsequently this matter is mixed with saliva and forms a dissolved liquid matter which is sucked up. A side benefit of the aforementioned stylet movement is that non-digestible chitin is not ingested (Cohen 1990).

4.3.6 Correlation of relationship of host plants and host

The enormous diversity of host plants and herbivorous Hemiptera causes the question whether closely related phytophagous insect groups feed on different plant lineages or if distantly related insect groups feed on the same plant. Jermy (1984) outlined four different types of insect-host plant-relationships. Type A including the majority of phytophagous insects comprises closely related monophagous or oligophagous species feeding on distantly related plants. This type is characteristic for Cicadidae, Coccoidea and Aphididae. Type B describes closely related oligophagous insect species feeding on plants of the same genus or family. It is present is some Coccoidea. Type C is the rarest one comprising closely related monophagous insect species feeding also on closely related plant species. This applies the obscure “pine aphids” (Adelgidae, Aphidoidea) feeding on conifers. Type D considers polyphagous insect species feeding on distantly related plants, e.g. some Pentatomidae, holocyclic Aphididae, and Cicadomorpha (except Cicadidae). The explanation for those different restricted feeding strategies is likely due to stenophagy (feeding on plant species which are closely related). Jermy (1984) pointed out that only specialists are adapted completely on a specific ecological parameter, although such life style requires more energy to find the appropriate host plant. However, specialists are then capable to feed with more efficiency on this plant. Additionally, there is only a little chance to reverse the evolutionary process from a specialized feeder to a generalist feeder. Jermy (1984) also explained in the field of sequential evolution that phytophagous insects have to switchover continually to new hosts to keep up with the high radiation of angiosperms. The evolution of insect-host plant-

relationships is likely linked with the evolution of the chemosensitive receptors of the labium, the antenna and the (pre)cibarium which are essential for host plant selection (Jermy 1984).

4.3.7 Sucking mechanism

Few information in literature exists according the stroke rate of the salivary piston. It is of 1.7 Hz average in the phytophagous *Philaenus spumarius* (Mallone et al. 1999), and 0.51 Hz in the haematophagous *Rhodnius prolixus* STÅL, 1859 (Wenk et al. 2010). Naito (1977) carried out a study concerning the frequency of stylet insertion of *Nephotettix cincticeps* (UHLER, 1896) (Cicadellidae, Cicadomorpha) depending on the host plant, temperature and movement activity. This species pierces into the host tissue between ten to 40 times per day, which sums up to a total of more than 12500 insertions a life time.

4.3.8 Interpretations of the evolution of feeding habits

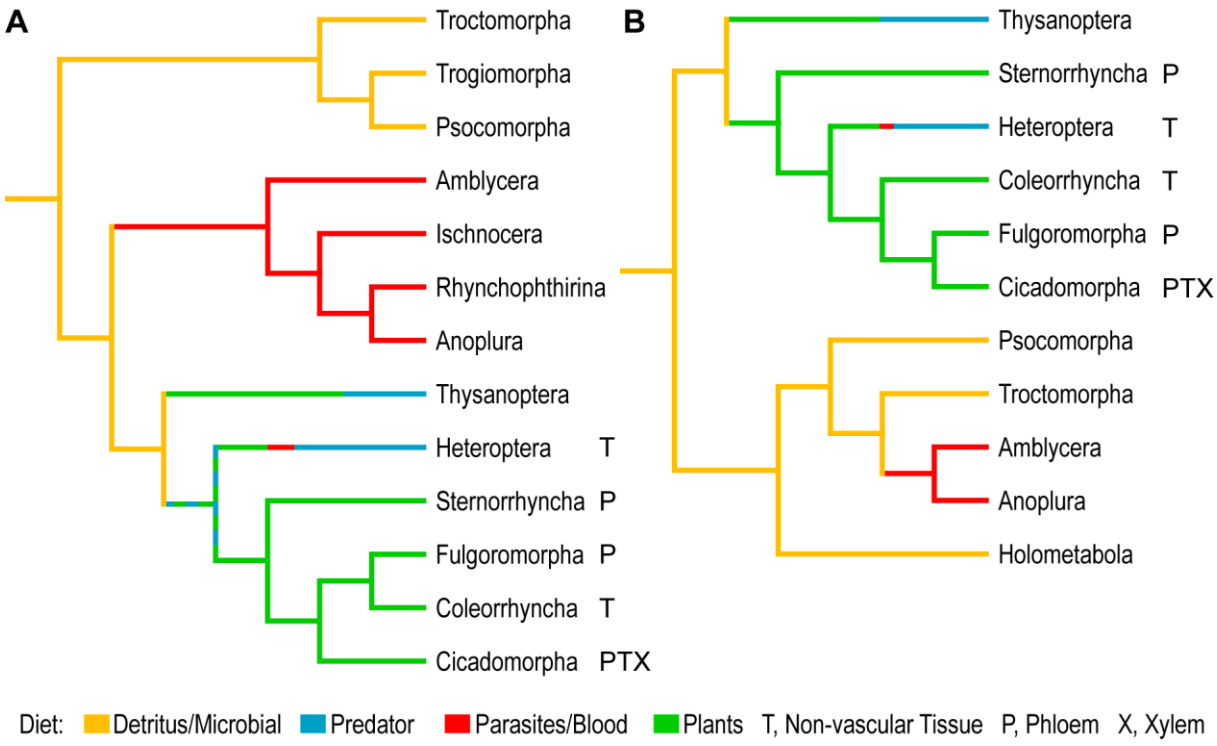

Figure 31 (previous page). Relationships of acercarian taxa with feeding habits mapped on the trees, modified after Novotny & Wilson (1997) and Grimaldi & Engel (2005). A: Phylogeny resulting from the data analyzed in the present study (see Fig. 29). Ancestral feeding mode of Hemiptera ambiguous (see also Mound & Heming [2000], Brodbeck et al. [2002], and Grimaldi & Engel [2005]). B: feeding modes mapped on phylogeny based on analyses of transcriptomes (Misof et al. subm.; 1KITE project) (see also Mound & Heming [2000], Brodbeck et al. [2002], and Grimaldi & Engel [2005]).

The phylogeny suggested by the results of the present study (Fig. 29) implies that the original diet of detritus or microbial matter was maintained in Psocoptera and apparently in the ancestors of Condylognatha (see also Sweet [1979] for ancestral feeding on eggs or inactive prey which can be considered as a kind of detritus; Mound & Heming 2000) (Fig. 31A). The branching pattern shown in Fig. 31A suggests that parasitism and blood feeding evolved two times independently, in Phthiraptera and in a single small subgroup of Heteroptera, respectively. The phylogeny remains ambiguous with respect to the ancestral feeding mode of Hemiptera (indicated by the green-blue-dotted line in Fig. 31A). Two scenarios are equally parsimonious. The proto-hemipteran could have been predaceous with this feeding habit maintained in Heteroptera and lost once in the stem group of (Sternorrhyncha + (Cicadomorpha + (Fulgoromorpha + Coleorrhyncha))), or it was phytophagous and the predaceous life style evolved once in Heteroptera and was secondarily abandoned within this group.

Mapping the feeding modes on a cladogram based on analyses of transcriptome data in the 1KITE project (www.1KITE.com, B. Misof et al., submit.) yielded a less ambiguous picture of the ancestral hemipteran and heteropteran diet (Fig. 31B). Ancestral Psocodea were detritophagous like the extant paraphyletic “Psocoptera”. That parasitism and blood feeding evolved two times independently within the two lineages (Amblycera + Anoplura) and Heteroptera was confirmed. The ancestral feeding habit of Thysanoptera is also considered as detritophagous (see Mound & Heming 2000). Phytophagous feeding habit is the most parsimonious interpretation for the ancestral feeding mode of Hemiptera and also for Heteroptera. This implies a herbivorous hemipteran ancestor with the single development of predaceous habits in Heteroptera. The opposite scenario of a predaceous ancestor would assume a multiple loss of carnivory in Sternorrhyncha and in the stem group of (Coleorrhyncha + Auchenorrhyncha), which appears as an unlikely evolutionary scenario.

Both cladograms (Figs. 31A,B) do not resolve the original precise food substrate in the case of herbivorous Hemiptera. Obligatory feeding on phloem cells is either part of the ground plan with a switch to non-vascular tissue feeding in Coleorrhyncha and Heteroptera, and xylem-sucking or mesophyll-sucking in single taxa of Cicadomorpha, respectively (phloem-feeding maintained in Cicadelloidea). Alternatively, phloem-sucking could have

evolved three times independently in Sternorrhyncha, Fulgoromorpha, and Cicadelloidea, assuming mesophyll as the ancestral host tissue (see also Novotny & Wilson 1997).

Mapping the diets on the cladograms also showed that there is no general correlation between the feeding habit and the orientation of the head (see also Wipfler 2012). Prognathy can be linked with both detrivory (Troctomorpha) and feeding on blood (Anoplura, Heteroptera). A hypognathous condition occurs not only in phytophagous species (e.g. Sternorrhyncha), but also in predators (some Thysanoptera) and in detrivores (ancestral feeding habit in Thysanoptera, see also Mound & Heming [2000]).

4.4 Conclusions and outlook

As extensively demonstrated in other studies (e.g. Beutel et al. 2010; Wipfler et al. 2011; Friedemann et al. 2012) cephalic characters provide valuable information for the reconstruction of the higher-level phylogeny of insect groups. However, an aspect often neglected in morphological studies is the individual variability of the specimen. Chaudonneret (1950) for example showed the tremendous variability of the hypopharyngeal suspensorial sclerites in a single species of *Thermobia* (Lepismatidae, Zygentoma). Backus & McLean (1983) investigated in their study ten to 25 specimens per hemipteran species which is of exemplary manner. The use of more than one specimen was aspired in the present study where possible (e.g. *Pediculus*, *Pseudococcus*) to reduce the significance of the individual variability. Nevertheless, especially in the case of writing theses this is an additional investment of much time and money.

Acercaria was strongly confirmed as monophyletic unit, whereas evidence for a sister group relationship with Zoraptera forming “Paraneoptera” is absent. The major nodes of the higher level-phylogeny of Acercaria could be solved. This refers in particular to the establishment of the clade Condylognatha. An extension of the taxon sampling and character matrix of the head in comparison to a previous study of Spangenberg et al. (2013a) rendered “Heteropterodea” as non-monophyletic. The key taxon Coleorrhyncha is nested within “Auchenorrhyncha” and corroborated the paraphyly of the latter. The monophyly of the traditional clade Phthiraptera including Amblycera is unambiguously supported. The monophyly of Psocoptera is also tentatively confirmed. However, a paraphyletic placement of “Psocodea” is ambiguous and likely an artifact as support of this scenario is found nowhere else in morphological or molecular studies. Current cladistic analyses of transcriptomic data of unprecedented extant (Misof et al. subm.) revealed instead Acercaria as paraphyletic and Auchenorrhyncha as monophyletic. Thus, the monophyly of both groups remains an open question.

Despite these new insights into Acercaria phylogeny the use of the head as a single character system is limited. Cephalic characters are apparently only partly suited to resolve subordinal relationships. This refers in particular to the phylogeny of Heteroptera (see Spangenberg et al. 2013b) and Cicadomorpha. However, both lineages and Hemiptera in general are strongly affected by homoplasious changes and functional constrains. The folding of the antennae below the head into a groove formed by the gena for instance is likely due to convergent evolution in Coleorrhyncha, Nepomorpha, and Amblycera due to similar ecological constrains to hide the antenna which would hinder the movement in moss cushion, water or hairs and feathers, respectively. Wipfler (2012) outlined in detail for Polyneoptera the limited cladistic evaluation as these constrains reduce the number of phylogenetically relevant characters on the one hand, and the high degree of correlation between feeding habit and mandibular shape reduces the significance of the latter character complex on the other. These findings are also applicable for Acercaria. However, the evaluation of mandibular, maxillary and labial evolution is far from being settled. This is due to the tremendous modifications of the mouth part structures. The generalized mandible is flattened and characterized by a dicondylic articulation. That of Condylognatha is transformed into a stylet articulated within the head capsule. Additionally, in Hemiptera specialized mandibular protractor muscles developed linked with a mandibular lever and mandibular plate. The elongated lacinia of Acercaria is detached from the stipes and its base tends to situated within the lumen of the head capsule. The mandibular and maxillary levers are evolutionary speaking new structures and likely evolved for indirect movement and guiding of the feeding stylets. The homology of the corresponding protractors and retractors is unclear. So far there is apparently no further evolutionary trend in Acercaria to reduce the mandibular musculature (see Wipfler 2012). This trend is recognizable considering the maxillary and hypopharyngeal muscles with special focus on Condylognatha. The evolution of the tube-like hemipteran labium is especially obscure and allows no estimation towards the evolution of its musculature. The present study outlined different hypotheses concerning possible homologies ranging from an origin from the prementum (basal segment) and labial palps (distal segments) (Matsuda 1965) over the development from the postmentum (basal segment) and prementum (second segment) (e.g. Pesson 1944; Poisson 1951) to the transformation of the submentum (basal segment), the mentum (the second segment), the prementum (third segment) and the glossae and paraglossae (apical segment).

The aim of a subsequent study would be to fill the morphological gaps of those species in the taxon sampling with unknown character state (e.g. ultrastructure of the antennae and compound eyes), and further to elucidate theirs glandular tissues associated with the mouthparts (e.g. maxillary and mandibular glands) or the nervous system (see. 8.3).

In the face of the increasing capabilities of new innovative morphological techniques, i.a Synchrotron radiation based Micro-Computer Tomography (SR-μCT) (e.g. Blanke & Thelen 2011) and molecular approaches (http://www.1kite.org/) it is essential to create a holistic data matrix including also all tagmata of the insect body ("total evidence" approach, e.g. Kluge 1989, 1998) to reconstruct a robust phylogeny with a stable reconstruction of evolutionary changes (see Wipfler 2012). It is evident that during character combination morphological features may get lost in the mass of molecular data (e.g. almost 460.000 amino acid sites in the study of Misof et al. subm.). However, these characters should be further applied in the cladistic analysis as they are elementary to reconstruct a morphological ground plan and help to visualize and illustrate substantial evolutionary steps in the amazing world of insects.

5. Summary

The present study is focused on five main issues, that is (1) a detailed documentation of the head morphology of a broad and representative Acercaria taxon sampling; (2) a reconstruction of the higher-lever phylogeny of Acercaria; (3) an evaluation of the evolution of cephalic characters, referring in particular to the hemipteroid assemblage; (4) a discussion of ecological aspects with special emphasizes on feeding habits and the diet; and (5) a consideration of functional aspects referring to the ingestion and the formation of salivary sheaths.

Cephalic features of 18 species were analyzed in detail including the key taxa Coleorrhyncha (Study I), Enicocephalomorpha, Dipsocoromorpha (Heteroptera) (Study III), and *Liposcelis* (Troctomorpha) (Study II). Data of additional 54 taxa was obtained from literature. The combination of both data sets yielded a character matrix with 397 potentially phylogenetic relevant characters for 72 specimens.

The result of the cladistic analysis of cephalic characters supported the monophyly of Acercaria with the simplified branching pattern (Troctomorpha + (Trogiomorpha + Psocomorpha)) + ((Amblycera + (Ischnocera + (Rhynchophthirina + Anoplura))) + (Thysanoptera + (Heteroptera + (Sternorrhyncha + ((Fulgoromorpha + Coleorrhyncha) + Cicadomorpha))))). The monophyly of the traditional subgroups Psocoptera, Phthiraptera, Thysanoptera, and Hemiptera is also supported. The paraphyly of “Psocodea” is ambiguous whereas the clade Condylognatha is considered as established. The internal phylogeny of Hemiptera showed “Auchenorrhyncha” (= Cicadomorpha + Fulgoromorpha), “Heteropterodea” (= Heteroptera + Coleorrhyncha), “Psyllomorpha” (= Psylloidea + Aleyrodoidea), and “Aphidomorpha” (= Aphidoidea + Coccoidea) are paraphyletic. The present study gave no evidence to a placement of Zoraptera as sister group to Acercaria (= “Paraneoptera”). Important non-homoplasious potential apomorphies of the major nodes are summarized in the following: **Acercaria:** internal articulation of lacinia; lacinia stylet-like and detached from stipes; cardo absent; absence of 0mx1 (M. craniocardinalis), 0mx3 (M. tentoriocardinalis), and 0mx9 (M. stipitopalpalis medialis); labial palp composed of a single segment; ventral orientation of floor of foodpump; **Psocoptera:** basal collar of antennomere three (and more distal segments in adults) as rupture-facilitating device; tri-furcated tip of lacinia; **Trogiomorpha + Psocomorpha:** length of oral hypopharyngeal arm shorter than length of sitophore (or body of hypopharynx); **Condylognatha + Phthiraptera:** insertion of 0md4 (M. hypopharyngomandibularis) restricted to posterior outer edge of mandibular lumen; 0mx12 (M. palpopalpalis maxillae primus) absent; contraction of labium during initialization of feeding; **Phthiraptera:** compound eye composed of two ommatidia; **Ischnocera + (Anoplura + Rhynchophthirina):** stipes not developed as well defined element; **Anoplura + Rhynchophthirina:** presence of antennal pore organs; mandibles and maxillae shifted craniad and theirs articulations are in or anterad

level of hypopharyngeal tip; 0mx6 (M. stipitolacinialis) absent; labrum equipped with teeth; “Mundvorraum” present; **Condylognatha:** pleurostomal ridge absent; mandible stylet-like; mandibles with piercing function; mandibular gnathal pouche present; laciniae grooved to form one or two canal(s) in interlocked condition; maxillary lever present; labrum narrowed, triangular, tongue-shaped; hypopharynx not tongue-shaped; sitophore of hypopharynx developed as salivary pumping chamber; piston present; suspensorium elongated and wing-like; hypopharynx with grooves as guiding devices for mandibles and maxillae; inter-pharyngeal locking mechanism present; **Hemiptera:** presence of two ocelli; mandibular plates (lora) present; condylus of mandibular base absent; mandibles symmetric; mandible or mandibular stylet encircles lacinia; barb-like structures at mandibular tip; mandibular lever present; labium forms a tube-like sheath for mandibles and laciniae; prementum not folded to form a salivary canal; formation of salivary pumping chamber or salivarium hypopharyngeal; opening of salivarium or pumping chamber located between maxillary stylets; **Sternorrhyncha + ((Fulgoromorpha + Coleorrhyncha) + Cicadomorpha):** ldvmx1 (“M. pronoto-tentorialis primus”) present.

Acercaria displays a broad array of mouthpart structures. The mouthparts of Psocoptera are only weakly modified showing reduced labial palps and chisel-shaped laciniae detached from the stipes. Peculiar and rather complex features of Pscoptera and Phthiraptera are the mortar and pestle apparatus, and the unique hypopharyngeal water-vapor uptake facility developed from the lingual sclerites. Chewing-biting mandibles are maintained in Psocoptera, Amblycera and Ischnocera. Maxillary palps are still present in Amblycera whereas they are absent in Ischnocera. The head of Anoplura is just totally free of labial and maxillary palps. Piercing-sucking mouthparts evolved three times independently within Acercaria. That is in two genera of Amblycera (one-pieced organ composed of the posterior arms of the hypopharynx), Anoplura (complex tripartite sting composed of the ventral part of the hypopharynx, the prementum and a salivary stylet with either hypopharyngeal or labial origin), and Condylognatha. Maxillary and labial palps are multiple-segmented in Thysanoptera whereas they are absent in the sister group Hemiptera. The third way of piercing-sucking mouthparts is shown in Condylognatha with stylet-like mandible(s) and laciniae. The evolution from a biting-chewing ancestor to a piercing-sucking hemipteran insect requires three putative stages. In a first step the clypeus and the cibarial dilatators are enlarged. The modifications during the second stage are more complex including the evolution of a hypognathous mouthcone linked with the narrowing of the labium and labrum, the reduction of the size of the maxillary and labial palps, and the transformation of the mandible and lacinia into slender stylets with an internal articulation. Simple mandibular and maxillary levers also evolved during this stage as elaborations of the respective gnathal pouch. The evolution of the hemipteran mandibular plate and the transformation of the stipes into the

maxillary plate (appendicular concept) are apparently established between stages two and three. In the third stage the modifications of the tube-like labium and of the stylet levers are finished, labial and maxillary palps are completely lost. The structure of the tentorium shows no unequivocal evolutionary trend and is highly variable within Condylognatha. The morphological transformation of the hypopharynx in Thysanoptera and Hemiptera comprises the reduction of the oral, loral, and posterior arms, the extension of the suspensorial sclerites (hypopharyngeal wings) and the reduction of the musculature.

The high diversification of the predominately phytophagous Hemiptera is apparently correlated with the radiation of plants. Relatively species-poor Psocoptera shows less specialized mouthparts and is characterized by a detritophagous or microbial diet which is close to the ancestral feeding habit. The presumable sister group Phthiraptera is exclusively parasitic feeding either on hairs or feathers (Amblycera, Ischnocera) or sucking blood by three different manners (piercing in Anoplura and two genera of Amblycera, lacerating in Rhynchophthirina). The ancestor of Thysanoptera and likely Condylognatha was detritophagous, whereas the former than refined a predatory and phytophagous life style during evolution (punching and sucking). The ancestral feeding habit of Hemiptera tentatively tends towards phytophagy, but carnivory cannot be excluded completely. Considering phylogenetic data showed the most parsimonious explanation of the ancestral herbal host tissue is either phloem or mesophyll. In Heteroptera blood feeding evolved a second time independently within Acercaria. A correlation between the feeding habit and the orientation of the head capsule is absent. The formation of salivary sheaths as guiding device for the labium and feeding stylets is arguably a ground plan character of Hemiptera. In general, the salivary sheaths of Heteroptera are unbranched and grafted outside the host tissue, whereas those of “Auchenorrhyncha” and Sternorrhyncha extend into the plant and branch out. The character state of Coleorrhyncha is presently unclear. Correlations of relationships of host and host plant are mixed within Acercaria ranging from closely related monophagous or oligophagous species feeding on distantly related plants over closely related monophagous species feeding on closely related plants to polyphagous insects feeding on distantly related plants.

The evolution of Acercaria shows a trend to reduce the maxillary musculature, with further reductions of the hypopharyngeal muscles, and the labial and maxillary palps in Hemiptera. In the latter the mandible developed into a stylet-like piercing organ linked with the mandibular lever and the mandibular plate. Both feeding stylets are hosted in a tube-like rostrum equipped with a complex longitudinal and transversal musculature. These tremendous transformations impede an evaluation of the character evolution as the homology in comparison to a generalized insect is vague. In the future a combined data matrix including all morphological characters of the insect body and EST data sets of 1KITE could help to uncover these last secrets and shed further light on the evolution of the Acercaria lineage.

6. Zusammenfassung

Die vorliegende Arbeit umfasst fünf thematische Schwerpunkte, das sind (1) die detaillierte Dokumentation der Kopfmorphologie repräsentativer Arten der Acercaria; (2) die phylogenetische Rekonstruktion deren höherer Verwandtschaftsverhältnisse; (3) die Beurteilung der Evolution wichtiger Kopfmerkmale, speziell in der Gruppe der Condylognatha; (4) die Diskussion ökologischer Aspekte mit besonderem Bezug auf die Ernährung und Ernährungsgewohnheiten; und (5) die Beurteilung funktioneller Aspekte im Hinblick auf die Nahrungsaufnahme und die Ausbildung von Sekretscheiden.

Die Kopfmerkmale von 18 Arten wurden im Detail untersucht. Dies beinhaltet den Einbezug der wichtigen Schlüsselgruppen Coleorrhyncha (Publikation I), Enicocephalomorpha, Dipsocoromorpha (Heteroptera) (Publikation III), und *Liposcelis* (Troctomorpha) (Publikation II). Die Merkmale von weiteren 54 Arten wurden aus Originalpublikationen entnommen. Beide Datensätze wurden zu einer Gesamtmatrix von 397 potentiell phylogenetisch relevanten Merkmalen für 72 Spezies zusammengefügt.

Das Ergebnis der kladistischen Analyse unterstützt die Monophylie der Acercaria und ergibt das folgende vereinfachte Verzweigungsmuster: (Troctomorpha + (Trogiomorpha + Psocomorpha)) + ((Amblycera + (Ischnocera + (Rhynchophthirina + Anoplura))) + (Thysanoptera + (Heteroptera + (Sternorrhyncha + ((Fulgoromorpha + Coleorrhyncha) + Cicadomorpha))))). Die Monophylie der traditionellen Untergruppen Psocoptera, Phthiraptera, Thysanoptera, und Hemiptera wird ebenfalls gestützt. Ein Paraphylum „Psocodea“ erscheint zweifelhaft während der Stamm Condylognatha als gesichert gilt. Die Phylogenie der Hemiptera verdeutlicht, dass “Auchenorrhyncha” (= Cicadomorpha + Fulgoromorpha), “Heteropterodea” (= Heteroptera + Coleorrhyncha), “Psyllomorpha” (= Psylloidea + Aleyrodoidea), und “Aphidomorpha” (= Aphidoidea + Coccoidea) als paraphyletisch zu betrachten sind. Morphologische Hinweise für ein Schwestergruppenverhältnis von Zoraptera + Acercaria (= Paraneoptera) fehlen. Im Folgenden werden wichtige potentielle, nicht auf Homoplasie beruhende Apomorphien der Hauptverzweigungspunkte zusammengefasst: **Acercaria:** interne Artikulation der Lacinia; Lacinia stilettförmig und abgelöst vom Stipes; Cardo fehlt; Fehlen von 0mx1 (M. craniocardinalis), 0mx3 (M. tentoriocardinalis), und 0mx9 (M. stipitopalpalis medialis); Labialpalpus eingliedrig; ventrale Ausrichtung des Bodens der Nahrungspumpe; **Psocoptera:** „Sollbruchstelle“ an der Basis des dritten Antennengliedes und darüber hinaus in Imagines; Apex der Lacinia dreizipfelig; **Trogiomorpha + Psocomorpha:** Länge des oralen hypopharyngealen Arms kürzer als die Länge der Sitophore bzw. des Hypopharynxkörpers; **Condylognatha + Phthiraptera:** Insertion des 0md4 (M. hypopharyngomandibularis) auf die Außenkante des Mandibelhohlraums begrenzt; 0mx12 (M. palpopalpalis maxillae primus) fehlt; Kontraktion des Labiums zur Einleitung der Nah-

rungsaufnahme; **Phthiraptera:** Komplexauge aus 2 Ommatidien bestehend; **Ischnocera + (Anoplura + Rhynchophthirina):** Stipes nicht als wohlumrissene Struktur ausgebildet; **Anoplura + Rhynchophthirina:** Vorhandensein von porenförmigen Organen auf der Antenne; Mandibeln und Maxillen nach cranial verlagert, sodass sie auf Höhe bzw. kurz vor der Spitze des Hypopharynx artikulieren; 0mx6 (M. stipitolacinialis) fehlend; Labrum mit Zähnchen versehen; „Mundvorraum“ vorhanden; **Condylognatha:** Pleurostomalleiste fehlend; Mandibel stilettförmig mit stechender Funktion; Mandibelsack vorhanden; Laciniae mit Rillen, die im verbundenen Zustand einen oder zwei Kanäle formen; maxillärer Hebel vorhanden; Labrum nach cranial verschmälert und zungenförmig; Hypopharynx nicht zungenförmig; Sitophore des Hypopharynx als Kammer der Speichelpumpe ausgebildet; Speichelkolben vorhanden; Suspensorium verlängert und flügelförmig; Hypopharynx mit Rillen als Führungseinrichtung für die Mandibeln und Maxillen; interpharyngealer Verriegelungsmechanismus vorhanden; **Hemiptera:** zwei Ocelli vorhanden; Mandibuläre Platten vorhanden; Condylus der Mandibelbasis fehlend; Mandibel symmetrisch; Mandibel umschließt die Lacinia; widerhakenförmige Strukturen am Apex der Mandibel; mandibulärer Hebel vorhanden; Labium als röhrenförmige Scheide für die Mandibeln und Laciniae; Prämentum nicht zum Speichelkanal gefaltet; Speichelpumpenkammer hypopharyngealen Ursprungs; Öffnung des Salivariums bzw. der Speichelpumpenkammer zwischen den maxillären Stiletten; **Sternorrhyncha + ((Fulgoromorpha + Coleorrhyncha) + Cicadomorpha):** ldvmx1 (“M. pronoto-tentorialis primus”) vorhanden.

Die starke Diversifikation der vorwiegend phytophagen Hemiptera korreliert vermutlich mit der Radiation der Pflanzen. Die Mundwerkzeuge der relativ artenarmen Psocoptera zeigen die geringsten Abwandlungen, jedoch mit bereits reduzierten Labialpalpen und von den Stipites losgelösten meißelförmigen Laciniae. Auffällige und sehr komplexe Gebilde der Phthiraptera und Psocoptera sind der Mörser-Pistill-Apparat sowie die einzigartige hypopharyngeale Vorrichtung zur Wasserdampfaufnahme, welche aus den Lingualskleriten hervorgegangen ist. Beißend-kauende Mandibeln wurden beibehalten in den Psocoptera, Amblycera und Ischnocera. Maxillarpalpen sind bei den Amblycera noch vorhanden, bei den Ischnocera aber bereits verloren gegangen. Der Kopf der Anoplura ist schließlich vollkommen frei von Labial- und Maxillarpalpen. Stechend-saugende Mundwerkzeuge evolvierten dreimal unabhängig innerhalb der Acercaria: in zwei Gattungen der Amblycera (einteiliges Organ bestehend aus den hypopharyngealen posterioren Armen), Anoplura (komplexer dreiteiliger Stachel aus dem ventralen Hypopharynx, dem Prämentum sowie einem Speichelstilett mit entweder labialem oder hypopharyngealem Ursprung) und Condylognatha. Die Maxillar- und Labialpalpen der Thysanoptera sind vielgliedrig, jedoch fehlend in der Schwestergruppe Hemiptera. Die stechend-saugenden Mundwerkzeuge der Condylognatha gehen aus stilettförmigen Mandibeln und Laciniae hervor. Die Evolution von einem beißend-

kauend Vorfahren zu einem stechend-saugenden hemipteren Insekt erfordert drei Schritte. Im ersten Schritt vergrößern sich der Clypeus sowie die an ihm ansetzenden cibarialen Dilatatoren. Die Modifikationen im zweiten Schritt sind deutlich komplexer und umfassen die Evolution eines hypognathen Mundkegels verbunden mit der Verschmälerung von Labium und Labrum, die Reduzierung der Größe von Labial- und Maxillarpalpen, und die Transformation von Mandibel und Lacinia in schlanke Stilette verbunden mit einer Artikulation im Kopfinneren. Einfache mandibuläre und maxilläre Hebel als jeweilige Ausstülpungen des Stilettsackes evolvierten ebenfalls in diesem Schritt. Die Evolution der mandibulären Platte sowie die Transformation des Stipes in die maxillare Platte (appendicular concept) fand vermutlich zwischen Schritt zwei und drei statt. Im dritten Stadium sind Modifikationen des röhrenförmigen Labiums und der Hebel abgeschlossen, Labial- und Maxillarpalpen sind vollständig reduziert. Die Struktur des Tentoriums zeigt keinen eindeutigen evolutionären Trend und ist innerhalb der Acercaria sehr variabel. Die morphologische Umwandlung des Hypopharynx bei Thysanoptera und Hemiptera umfasst die Reduktion der oralen, loralen und posterioren Arme, die Erweiterung der suspensorialen Sklerite (Hypopharynxflügel) und die Reduktion der Muskulatur.

Die große Diversität der Mundwerkzeuge erwächst aus den vielfältigen Ernährungsweisen. Psocopteren sind nur wenig spezialisiert und ernähren sich von Detritus was eng an die ursprüngliche Nahrungsgewohnheit angelehnt ist. Die mutmaßliche Schwestergruppe der Phthiraptera lebt ausschließlich parasitär von Haaren oder Federn (Ischnocera, Amblycera) oder saugt auf drei verschiedene Arten Blut (stechend in Anoplura und zwei Gattungen Amblycera, kratzend und oberflächliche Wunden verursachend in Rhynchophthirina). Der Vorfahre der Thysanoptera und wahrscheinlich auch Condylognatha fraß Detritus, wobei erstere dann während der Evolution Phytophagie und Carnivorie (stoßend-saugend) verfeinerten. Die ursprüngliche Ernährungsweise der Hemiptera tendiert vermutlich in Richtung Phytophagie, jedoch kann Carnivorie nicht vollkommen ausgeschlossen werden. Betrachtet man das Kladogramm so erscheinen im Falle eines herbivoren Vorfahrens sowohl Phloem als auch Mesophyll als ursprüngliche Wirtsgewebe gleich wahrscheinlich. In den echten Wanzen entwickelte sich zum zweiten male unabhängig das Blutsaugen innerhalb der Acercaria. Ein genereller Zusammenhang zwischen der Ernährungsweise und der Ausrichtung der Kopfkapsel besteht jedoch nicht. Die Bildung von Sekretscheiden als Führungshilfe für das Labium und die Stechborsten ist ein Merkmal im Grundmuster der Hemiptera. Die Scheiden der Heteroptera sind dabei unverzweigt und auf die Wirtsoberfläche aufgesetzt während diejenigen der Sternorrhyncha und „Auchenorrhyncha“ auch in das Wirtsmedium reichen und sich dort verzweigen. Die Ausprägung dieses Merkmals innerhalb der Mooswanzen ist derzeit unklar. Die Frage ob eng verwandte Insektenarten sich auch von eng verwandten Pflanzenarten ernähren bzw. anders herum kann nicht eindeutig

beantwortet werden. Es gibt beispielsweise sowohl eng verwandte mono- bzw. oligophage Arten, die auf weit entfernt verwandten Pflanzenarten leben als auch monophage Arten, die sich von eng verwandten Pflanzen ernähren.

Die Evolution der Acercaria zeigt einen Trend zur Reduktion der maxillären Muskulatur mit fortschreitender Minimierung der Hypopharynxmuskeln, Labial- und Maxillarpalpen in den Hemipteren. Bei letzteren bildete sich die Mandibel zu einem Stechorgan um, das in enger Verbindung mit dem mandibulären Hebel sowie der mandibulären Platte steht. Die Stechborsten liegen in einem röhrenförmigen Labium, das mit einer komplexen Längs- und Quermuskulatur ausgestattet ist. Diese enormen Umwandlungen erschweren eine Beurteilung der Merkmalsevolution. Die Homologisierung der Muskulatur im Vergleich zu einem generalisierten Insekt ist unklar. In der Zukunft könnte eine ganzheitliche kombinierte Datenmatrix basierend auf sämtlichen morphologische Merkmalen des Insektenkörpers sowie seiner molekularen Marker (1KITE) helfen, diese letzten Geheimnisse zu lüften und so ein neues Licht auf die Evolutionsgeschichte der Acercaria werfen.

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8. Appendix

8.1 Appendix 1

Homologization of cephalic muscles described in different studies following Friedrich & Beutel (2008) and Wipfler et al. (2011). Abbreviations: +, muscle present in one of the species included in the present study (or described in another study without specific abbreviation); -, muscle absent; /, muscle not covered in a study, present or absent; ?, unclear homology

Muscles of the antenna

0an1, M. tentorioscapalis anterior
Systelloderes (Spangenberg et al. 2013b): M6; *Cryptostemma* (Spangenberg et al. 2013b): M6; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): KM21; *Corixa* (Benwitz 1956): deprsc; *Gelastocoris* (Parsons 1959): KM21; *Lethocerus* (Parsons 1968): H21; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): M6; *Hydrometra* (Sprague 1956): ? (antennal muscles); *Saldula* (Parsons 1962): 21; *Triatoma* (Barth 1952a,b, 1953a,b): Mu14; *Dysdercus* (Kumari 1955): depressor; *Hackeriella* (Spangenberg et al. 2013a): M6; *Hemiodoecus* (Singh 1971): 1; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): m. ant3; *Macrosiphum* (Singh 1971): 1; *Dactylosphaera* (Rilling 1960): 15; *Trialeurodes* (Weber 1935): m. ant; *Aleurolobus* (Singh 1971): 1; *Aleyrodes* (present study [=ps in the following]): +; *Psylla* (Weber 1929): m. ant3; *Diaphorina* (Singh 1971): 1; *Cacopsylla* (ps): +; *Pseudococcus* (ps): + (Fig. 10C); *Perissopneumon* (Singh 1971): 1; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): 1; *Philaenus* (ps): +; *Lepyronia* (Kramer 1950): ? (mant) description unclear; *Platypleura* (Singh 1971): 1; *Oxyrhachis* (Singh 1971): 1; *Scolops* (Kramer 1950): mant; *Melicharia* (Singh 1971): 1; *Dictyophara* (ps): +; *Aeolothrips fasciatus* (Mickoleit 1963): 3; *Aeolothrips intermedius* (Moritz 1982b): M.3; *Thrips* (Risler 1957): 2; *Haplothrips* (Mickoleit 1963): 3; *Phlaeothrips* (Mickoleit 1963): 3; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): Y; *Caecilius* (ps): +; *Cerobasis* (ps): +; *Troctes* (Noland 1924): /; *Liposcelis* (ps): + (Figs. 18C,D,E); *Gliricola* (Risler & Geising 1965): + (see fig.3); *Myrsidea* (Buckup 1959): 2; *Pseudomenopon* (Haub 1967): 2; *Piagetiella* (ps): + (Figs. 20C,D); *Trochiloecetes* (Haub 1983): 2.1.2.1.; *Trimenopon* (Stöwe 1943): X; *Bovicola* (Risler 1951): 2; *Ornithobius* (Haub 1971): 4.1.1.1.; *Columbicola* (ps): + (Fig. 22D); *Haematopinus* (Ramcke 1965): /; *Hybophthirus* (Tröster 1990a): M2; *Pediculus* (ps): + (Fig. 25E); *Phthirus* (Hirsch 1986): /; *Haematomyzus* (Weber 1969): 2; *Macroxyela* (Beutel & Vilhelmsen 2007): M.2; *Osmylus* (Beutel et al. 2010): M2; *Schizodactylus* (Khattar 1964): 5; *Oniscigaster* (Staniczek 2001): M3; *Zorotypus* (Beutel & Weide 2005): M2; *Perla* (Chisholm 1962): A.D.M.

0an2, M. tentorioscapalis posterior
Systelloderes (Spangenberg et al. 2013b): M7; *Cryptostemma* (Spangenberg et al. 2013b): M7; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): KM20; *Corixa* (Benwitz 1956): lev?sc; *Gelastocoris* (Parsons 1959): KM20; *Lethocerus* (Parsons 1968): H20; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): M7; *Hydrometra* (Sprague 1956): ? (antennal muscles); *Saldula* (Parsons 1962): 20; *Triatoma* (Barth 1952a,b, 1953a,b): Mu13; *Dysdercus* (Kumari 1955): levator; *Hackeriella* (Spangenberg et al. 2013a): M7; *Hemiodoecus* (Singh 1971): 1; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): m. ant2; *Macrosiphum* (Singh 1971): 1; *Dactylosphaera* (Rilling 1960): 18; *Trialeurodes* (Weber 1935): m. ant; *Aleurolobus* (Singh 1971): 1; *Aleyrodes* (ps): +; *Psylla* (Weber 1929): m. ant2; *Diaphorina* (Singh 1971): 1; *Cacopsylla* (ps): +; *Pseudococcus* (ps): + (Fig. 10C); *Perissopneumon* (Singh 1971): 1; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): 1; *Philaenus* (ps): +; *Lepyronia* (Kramer 1950): ? (mant) description unclear; *Platypleura* (Singh 1971): 1; *Oxyrhachis* (Singh 1971): 1; *Scolops* (Kramer 1950): mant; *Melicharia* (Singh 1971): 1; *Dictyophara* (ps): +; *Aeolothrips fasciatus*

(Mickoleit 1963): 2; *Aeolothrips intermedius* (Moritz 1982b): M.4; *Thrips* (Risler 1957): 1; *Haplothrips* (Mickoleit 1963): 2; *Phlaeothrips* (Mickoleit 1963): 2; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): X; *Caecilius* (ps): +; *Cerobasis* (ps): + (Fig. 16C); *Troctes* (Noland 1924): /; *Liposcelis* (ps): + (Figs. 18D,E); *Gliricola* (Risler & Geising 1965): + (see fig.3); *Myrsidea* (Buckup 1959): 1; *Pseudomenopon* (Haub 1967): 1; *Piagetiella* (ps): + (Figs. 20C,D); *Trochiloecetes* (Haub 1983): 2.1.2.2.; *Trimenopon* (Stöwe 1943): Y; *Bovicola* (Risler 1951): 1; *Ornithobius* (Haub 1971): 4.1.1.2.; *Columbicola* (ps): + (Fig. 22E); *Haematopinus* (Ramcke 1965): /; *Hybophthirus* (Tröster 1990a): M1; *Pediculus* (ps): + (Fig. 25E); *Phthirus* (Hirsch 1986): /; *Haematomyzus* (Weber 1969): 1; *Macroxyela* (Beutel & Vilhelmsen 2007): M.1; *Osmylus* (Beutel et al. 2010): M1; *Schizodactylus* (Khattar 1964): 4; *Oniscigaster* (Staniczek 2001): M1; *Zorotypus* (Beutel & Weide 2005): M1; *Perla* (Chisholm 1962): A.E.M.

0an3, M. tentorioscapalis lateralis

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): ? (antennal muscles); *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Kumari 1955): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): m. ant4; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): 16; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): ? (mant) description in text unclear; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): Z; *Caecilius* (ps): +; *Cerobasis* (ps): + (Fig. 16C); *Troctes* (Noland 1924): /; *Liposcelis* (ps): + (Figs. 18C,D,E); *Gliricola* (Risler & Geising 1965): + (see fig.3); *Myrsidea* (Buckup 1959): 3; *Pseudomenopon* (Haub 1967): 3; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): 2.1.2.3.; *Trimenopon* (Stöwe 1943): Z; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): /; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): + (Fig. 25E); *Phthirus* (Hirsch 1986): /; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): M.3; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): M2; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): ? (A.E.M.)

0an4, M. tentorioscapalis medialis

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): ? (antennal muscles); *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Kumari 1955): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): m. ant1; *Macrosiphum* (Singh 1971): 1; *Dactylosphaera* (Rilling 1960): 17; *Trialeurodes* (Weber 1935): m. ant; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): +; *Psylla* (Weber 1929): m. ant1; *Diaphorina* (Singh 1971): 1; *Cacopsylla* (ps): +; *Pseudococcus* (ps): + (Fig. 10C); *Perissopneumon* (Singh 1971): 1; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): ? (mant) description in text unclear; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): mant; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -;

Phlaeothrips (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -.; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): /; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): /; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): M.4; *Osmylus* (Beutel et al. 2010): M4; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): M4 (homology implies a shift of insertion to the pedicellus); *Zorotypus* (Beutel & Weide 2005): M.4; *Perla* (Chisholm 1962): ? (A.E.M.)

0an5, M. frontopedicellaris
absent in all taxa examined and not mentioned in other studies

0an6, M. scapopedicellaris lateralis
Systelloderes (Spangenberg et al. 2013b): M8; *Cryptostemma* (Spangenberg et al. 2013b): M8; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): KM23; *Corixa* (Benwitz 1956): + (see fig. 13); *Gelastocoris* (Parsons 1959): KM23; *Lethocerus* (Parsons 1968): H23; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): M8; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): 23; *Triatoma* (Barth 1952a,b, 1953a,b): /; *Dysdercus* (Kumari 1955): intrinsic muscles; *Hackeriella* (Spangenberg et al. 2013a): M8; *Hemiodoecus* (Singh 1971): 2; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): /; *Macrosiphum* (Singh 1971): 2; *Dactylosphaera* (Rilling 1960): 21+22; *Trialeurodes* (Weber 1935): /; *Aleurolobus* (Singh 1971): 2; *Aleyrodes* (ps): +; *Psylla* (Weber 1929): /; *Diaphorina* (Singh 1971): 2; *Cacopsylla* (ps): +; *Pseudococcus* (ps): + (Fig. 10B); *Perissopneumon* (Singh 1971): 2; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): 2; *Philaenus* (ps): +; *Lepyronia* (Kramer 1950): /; *Platypleura* (Singh 1971): 2; *Oxyrhachis* (Singh 1971): 2; *Scolops* (Kramer 1950): /; *Melicharia* (Singh 1971): 2; *Dictyophara* (ps): +; *Aeolothrips fasciatus* (Mickoleit 1963): 4; *Aeolothrips intermedius* (Moritz 1982b): M.1; *Thrips* (Risler 1957): 3; *Haplothrips* (Mickoleit 1963): 4; *Phlaeothrips* (Mickoleit 1963): 4; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): musculature du pédicelle 1, 2, 3, 5; *Caecilius* (ps): +; *Cerobasis* (ps): + (Fig. 16B); *Troctes* (Noland 1924): /; *Liposcelis* (ps): + (Fig. 18C); *Gliricola* (Risler & Geising 1965): + (see fig. 3); *Myrsidea* (Buckup 1959): 4; *Pseudomenopon* (Haub 1967): 4; *Piagetiella* (ps): + (Fig. 20E); *Trochiloecetes* (Haub 1983): 2.1.2.4.; *Trimenopon* (Stöwe 1943): y1; *Bovicola* (Risler 1951): 3; *Ornithobius* (Haub 1971): 4.1.1.3; *Columbicola* (ps): + (Figs. 22D,E); *Haematopinus* (Ramcke 1965): /; *Hybophthirus* (Tröster 1990a): M3; *Pediculus* (ps): + (Fig. 25E); *Phthirus* (Hirsch 1986): /; *Haematomyzus* (Weber 1969): 4; *Macroxyela* (Beutel & Vilhelmsen 2007): M.5; *Osmylus* (Beutel et al. 2010): M5; *Schizodactylus* (Khattar 1964): 7; *Oniscigaster* (Staniczek 2001): ? (Staniczek (2001) assumed that the original intrinsic antennal muscles are fused with his M4 (M. tentorio-pedicellaris ventralis) as the latter reaches also into the pedicellus which is very atypical for an external antennal muscle); *Zorotypus* (Beutel & Weide 2005): M.5; *Perla* (Chisholm 1962): /.

0an7, M. scapopedicellaris medialis
Systelloderes (Spangenberg et al. 2013b): M9; *Cryptostemma* (Spangenberg et al. 2013b): M9; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): KM22; *Corixa* (Benwitz 1956): + (see fig. 13); *Gelastocoris* (Parsons 1959): KM22; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): M9; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): 22; *Triatoma* (Barth 1952a,b, 1953a,b): /; *Dysdercus* (Kumari 1955): intrinsic muscles; *Hackeriella* (Spangenberg et al. 2013a): M9; *Hemiodoecus* (Singh 1971): 2; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): /; *Macrosiphum* (Singh 1971): 2; *Dactylosphaera* (Rilling 1960): 19+20; *Trialeurodes* (Weber 1935): /; *Aleurolobus* (Singh 1971): 2; *Aleyrodes* (ps): +; *Psylla* (Weber 1929): /; *Diaphorina* (Singh 1971): 2; *Cacopsylla* (ps): +; *Pseudococcus* (ps): + (Fig. 10B); *Perissopneumon* (Singh 1971): 2; *Tibicina* (Snodgrass 1927; Kramer

1950): /; *Idiocerus* (Arora & Singh 1962): 2; *Philaenus* (ps): +; *Lepyronia* (Kramer 1950): /; *Platypleura* (Singh 1971): 2; *Oxyrhachis* (Singh 1971): 2; *Scolops* (Kramer 1950): /; *Melicharia* (Singh 1971): 2; *Dictyophara* (ps): +; *Aeolothrips fasciatus* (Mickoleit 1963): 5; *Aeolothrips intermedius* (Moritz 1982b): M.2; *Thrips* (Risler 1957): 4; *Haplothrips* (Mickoleit 1963): 5; *Phlaeothrips* (Mickoleit 1963): 5; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): musculature du pédicelle 4, 6, 7; *Caecilius* (ps): +; *Cerobasis* (ps): + (Fig. 16B); *Troctes* (Noland 1924): /; *Liposcelis* (ps): + (Figs. 18C,D); *Gliricola* (Risler & Geising 1965): + (see fig. 3); *Myrsidea* (Buckup 1959): 5; *Pseudomenopon* (Haub 1967): 5; *Piagetiella* (ps): + (Fig. 20E); *Trochiloecetes* (Haub 1983): 2.1.2.5.; *Trimenopon* (Stöwe 1943): x+z; *Bovicola* (Risler 1951): 4; *Ornithobius* (Haub 1971): 4.1.1.4; *Columbicola* (ps): + (Figs. 22D,E); *Haematopinus* (Ramcke 1965): /; *Hybophthirus* (Tröster 1990a): M4; *Pediculus* (ps): +; *Phthirus* (Hirsch 1986): /; *Haematomyzus* (Weber 1969): 3; *Macroxyela* (Beutel & Vilhelmsen 2007): M.6; *Osmylus* (Beutel et al. 2010): M6; *Schizodactylus* (Khattar 1964): 6; *Oniscigaster* (Staniczek 2001): ? (see **0an6, M. scapopedicellaris lateralis**); *Zorotypus* (Beutel & Weide 2005): M.6; *Perla* (Chisholm 1962): /.

0an8, M. intraflagellaris (primus)

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): M9; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): /; *Dysdercus* (Kumari 1955): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): 3; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): /; *Macrosiphum* (Singh 1971): 3; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): /; *Aleurolobus* (Singh 1971): 3; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): /; *Diaphorina* (Singh 1971): 3; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): 3; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): 3; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): /; *Platypleura* (Singh 1971): 3; *Oxyrhachis* (Singh 1971): 3; *Scolops* (Kramer 1950): /; *Melicharia* (Singh 1971): 3; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): /; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): /; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): ? (see **0an6, M. scapopedicellaris lateralis**); *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): /.

0anx1, "M. intraflagellaris secundus"

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): M9; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): /; *Dysdercus* (Kumari 1955): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): 3; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): /; *Macrosiphum* (Singh 1971): 3; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): /; *Aleurolobus* (Singh 1971): 3; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): /; *Diaphorina* (Singh 1971): 3; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): 3; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): 3; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): /; *Platypleura* (Singh 1971): 3; *Oxyrhachis* (Singh 1971): 3; *Scolops* (Kramer 1950): /; *Melicharia* (Singh 1971): 3; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -;

Aeolothrips intermedius (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): /; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): /; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): ? (see **0an6, M. scapopedicellaris lateralis**); *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): /.

Muscles of the antennal heart

absent in all taxa examined and not mentioned in other studies.

Muscles of the labrum

0lb1, M. frontolabralis

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): -; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): 6; *Aeolothrips intermedius* (Moritz 1982b): M.5; *Thrips* (Risler 1957): 19; *Haplothrips* (Mickoleit 1963): 6; *Phlaeothrips* (Mickoleit 1963): 6; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): a; *Caecilius* (ps): +; *Cerobasis* (ps): + (Fig. 16B); *Troctes* (Noland 1924): /; *Liposcelis* (ps): + (Figs. 18B,C); *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): 28; *Pseudomenopon* (Haub 1967): 28; *Piagetiella* (ps): + (Figs. 20B,C); *Trochiloecetes* (Haub 1983): 3.1.2.1.; *Trimenopon* (Stöwe 1943): a; *Bovicola* (Risler 1951): 26; *Ornithobius* (Haub 1971): 7.1.1.1.; *Columbicola* (ps): +; *Haematopinus* (Ramcke 1965): 1; *Hybophthirus* (Tröster 1990a): M5; *Pediculus* (ps): + (Fig. 25F); *Phthirus* (Hirsch 1986): M20; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): M8; *Schizodactylus* (Khattar 1964): 1; *Oniscigaster* (Staniczek 2001): M5; *Zorotypus* (Beutel & Weide 2005): M.8; *Perla* (Chisholm 1962): LR. EL.

0lb2, M. frontoepipharyngalis

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): -; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -;

Lepyronia (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): 11; *Aeolothrips intermedius* (Moritz 1982b): M.17; *Thrips* (Risler 1957): 20; *Haplothrips* (Mickoleit 1963): 11; *Phlaeothrips* (Mickoleit 1963): 11; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): b; *Caecilius* (ps): +; *Cerobasis* (ps): + (Fig. 16B); *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): 35; *Piagetiella* (ps): + (Figs. 20B,C); *Trochiloecetes* (Haub 1983): 3.2.2.1.; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): 32; *Ornithobius* (Haub 1971): 7.2.1.6.; *Columbicola* (ps): + (Fig. 22C); *Haematopinus* (Ramcke 1965): 4; *Hybophthirus* (Tröster 1990a): M7; *Pediculus* (ps): + (Figs. 25C,D); *Phthirus* (Hirsch 1986): M13; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): M.9; *Osmylus* (Beutel et al. 2010): M9; *Schizodactylus* (Khattar 1964): 2; *Oniscigaster* (Staniczek 2001): M6; *Zorotypus* (Beutel & Weide 2005): M.9; *Perla* (Chisholm 1962): LR. DEP.

0lb3, M. epistoepipharyngealis
absent in all taxa examined and not mentioned in other studies

0lb4, M. labralis transversalis
absent in all taxa examined and not mentioned in other studies

0lb5, M. labroepipharyngealis
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): -; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): 23; *Philaenus* (ps): +; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): 32; *Dictyophara* (ps): + (Fig. 14A); *Aeolothrips fasciatus* (Mickoleit 1963): 7; *Aeolothrips intermedius* (Moritz 1982b): M.6; *Thrips* (Risler 1957): 21; *Haplothrips* (Mickoleit 1963): 7; *Phlaeothrips* (Mickoleit 1963): 7; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): c; *Caecilius* (ps): +; *Cerobasis* (ps): +; *Troctes* (Noland 1924): /; *Liposcelis* (ps): +; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Buckup 1959): 29; *Pseudomenopon* (Haub 1967): 29; *Piagetiella* (ps): +; *Trochiloecetes* (Haub 1983): 3.1.2.2.; *Trimenopon* (Stöwe 1943): c; *Bovicola* (Risler 1951): 27a+b; *Ornithobius* (Haub 1971): 7.1.1.2.; *Columbicola* (ps): +; *Haematopinus* (Ramcke 1965): 2; *Hybophthirus* (Tröster 1990a): M6; *Pediculus* (ps): + (Figs. 25B,C,D); *Phthirus* (Hirsch 1986): M14; *Haematomyzus* (Weber 1969): 10; *Macroxyela* (Beutel & Vilhelmsen 2007): M.7; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): 3; *Oniscigaster* (Staniczek 2001): M7; *Zorotypus* (Beutel & Weide 2005): M.7; *Perla* (Chisholm 1962): CIB. DIL.

0lb6, M. labrolabralis
absent in all taxa examined and not mentioned in other studies

0lbx1, "M. longitudinalis epipharyngealis dorsalis"
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): -; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris*

(Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): 7.2.1.8.; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): 5; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): lm; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

0lbx2, "M. tentorio-epipharyngealis"

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): -; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): M.9; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): 35; *Phlaeothrips* (Mickoleit 1963): 35; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): 5; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

Muscles of the mandible

0md1, M. craniomandibularis internus

Systelloderes (Spangenberg et al. 2013b): ?; *Cryptostemma* (Spangenberg et al. 2013b): ?; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): ?; *Corixa* (Benwitz 1956): ?; *Gelastocoris* (Parsons 1959): ?; *Lethocerus* (Parsons 1968): ?; *Belostoma* (Verma et al. 1973): ?; *Hydrocyrius* (Kopelke 1978): ?; *Nepa* (Hamilton 1931, Rieger 1976): ?; *Gerris* (Spangenberg et al. 2013b): ?; *Hydrometra* (Sprague 1956): ?; *Saldula* (Parsons 1962): ?; *Triatoma* (Barth 1952a,b, 1953a,b): ?; *Dysdercus* (Khan 1972): ?; *Hackeriella* (Spangenberg et al. 2013a): ?;

Hemiodoecus (Singh 1971): ?; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): ?; *Macrosiphum* (Singh 1971): ?; *Dactylosphaera* (Rilling 1960): ?; *Trialeurodes* (Weber 1935): ?; *Aleurolobus* (Singh 1971): ?; *Aleyrodes* (ps): ?; *Psylla* (Weber 1929): ?; *Diaphorina* (Singh 1971): ?; *Cacopsylla* (ps): ?; *Pseudococcus* (ps): ?; *Perissopneumon* (Singh 1971): ?; *Tibicina* (Snodgrass 1927; Kramer 1950): ?; *Idiocerus* (Arora & Singh 1962): ?; *Philaenus* (ps): ?; *Lepyronia* (Kramer 1950): ?; *Platypleura* (Singh 1971): ?; *Oxyrhachis* (Singh 1971): ?; *Scolops* (Kramer 1950): ?; *Melicharia* (Singh 1971): ?; *Dictyophara* (ps): ?; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): +; *Psococerastis* (Masumoto & Nagashima 1993): 21; *Stenopsocus* (Badonnel 1934): M; *Caecilius* (ps): +; *Cerobasis* (ps): + (Figs. 4B, 16C,E); *Troctes* (Noland 1924): adductor muscle; *Liposcelis* (ps): + (Figs. 4A, 18G,H,I); *Gliricola* (Risler & Geising 1965): 1; *Myrsidea* (Buckup 1959): 7; *Pseudomenopon* (Haub 1967): 7; *Piagetiella* (ps): + (Figs. 20F,G,H); *Trochiloecetes* (Haub 1983): 2.2.2.1.; *Trimenopon* (Stöwe 1943): Add.; *Bovicola* (Risler 1951): 6; *Ornithobius* (Haub 1971): 4.2.1.2.; *Columbicola* (ps): + (Figs. 22F,G); *Haematopinus* (Ramcke 1965): 10; *Hybophthirus* (Tröster 1990a): M19; *Pediculus* (ps): + (Figs. 25E,F); *Phthirus* (Hirsch 1986): M1; *Haematomyzus* (Weber 1969): 6; *Macroxyela* (Beutel & Vilhelmsen 2007): M.11; *Osmylus* (Beutel et al. 2010): M11; *Schizodactylus* (Khattar 1964): 9; *Oniscigaster* (Staniczek 2001): M25; *Zorotypus* (Beutel & Weide 2005): M.11; *Perla* (Chisholm 1962): M. AD. M.

0md2, M. craniomandibularis externus anterior

Systelloderes (Spangenberg et al. 2013b): ?; *Cryptostemma* (Spangenberg et al. 2013b): ?; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): ?; *Corixa* (Benwitz 1956): ?; *Gelastocoris* (Parsons 1959): ?; *Lethocerus* (Parsons 1968): ?; *Belostoma* (Verma et al. 1973): ?; *Hydrocyrius* (Kopelke 1978): ?; *Nepa* (Hamilton 1931, Rieger 1976): ?; *Gerris* (Spangenberg et al. 2013b): ?; *Hydrometra* (Sprague 1956): ?; *Saldula* (Parsons 1962): ?; *Triatoma* (Barth 1952a,b, 1953a,b): ?; *Dysdercus* (Khan 1972): ?; *Hackeriella* (Spangenberg et al. 2013a): ?; *Hemiodoecus* (Singh 1971): ?; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): ?; *Macrosiphum* (Singh 1971): ?; *Dactylosphaera* (Rilling 1960): ?; *Trialeurodes* (Weber 1935): ?; *Aleurolobus* (Singh 1971): ?; *Aleyrodes* (ps): ?; *Psylla* (Weber 1929): ?; *Diaphorina* (Singh 1971): ?; *Cacopsylla* (ps): ?; *Pseudococcus* (ps): ?; *Perissopneumon* (Singh 1971): ?; *Tibicina* (Snodgrass 1927; Kramer 1950): ?; *Idiocerus* (Arora & Singh 1962): ?; *Philaenus* (ps): ?; *Lepyronia* (Kramer 1950): ?; *Platypleura* (Singh 1971): ?; *Oxyrhachis* (Singh 1971): ?; *Scolops* (Kramer 1950): ?; *Melicharia* (Singh 1971): ?; *Dictyophara* (ps): ?; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): -; *Psococerastis* (Masumoto & Nagashima 1993): -; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): -; *Liposcelis* (ps): + (Figs. 4A, 18B,C,E); *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): M26; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

0md3, M. craniomandibularis externus posterior

Systelloderes (Spangenberg et al. 2013b): ?; *Cryptostemma* (Spangenberg et al. 2013b): ?; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): ?; *Corixa* (Benwitz 1956): ?; *Gelastocoris* (Parsons 1959): ?; *Lethocerus* (Parsons 1968): ?; *Belostoma* (Verma et al. 1973): ?; *Hydrocyrius* (Kopelke 1978): ?; *Nepa* (Hamilton 1931, Rieger 1976): ?; *Gerris* (Spangenberg et al. 2013b): ?; *Hydrometra* (Sprague 1956): ?; *Saldula* (Parsons 1962): ?; *Triatoma* (Barth 1952a,b, 1953a,b): ?; *Dysdercus* (Khan 1972): ?; *Hackeriella* (Spangenberg et al. 2013a): ?; *Hemiodoecus* (Singh 1971): ?; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): ?; *Macrosiphum* (Singh 1971): ?; *Dactylosphaera* (Rilling 1960): ?; *Trialeurodes* (Weber 1935): ?; *Aleurolobus* (Singh 1971): ?; *Aleyrodes* (ps): ?; *Psylla* (Weber 1929): ?;

Diaphorina (Singh 1971): ?; *Cacopsylla* (ps): ?; *Pseudococcus* (ps): ?; *Perissopneumon* (Singh 1971): ?; *Tibicina* (Snodgrass 1927; Kramer 1950): ?; *Idiocerus* (Arora & Singh 1962): ?; *Philaenus* (ps): ?; *Lepyronia* (Kramer 1950): ?; *Platypleura* (Singh 1971): ?; *Oxyrhachis* (Singh 1971): ?; *Scolops* (Kramer 1950): ?; *Melicharia* (Singh 1971): ?; *Dictyophara* (ps): ?; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): +; *Psococerastis* (Masumoto & Nagashima 1993): 23; *Stenopsocus* (Badonnel 1934): N; *Caecilius* (ps): +; *Cerobasis* (ps): + (Figs. 4B, 16C,D); *Troctes* (Noland 1924): abductor muscle; *Liposcelis* (ps): + (Figs. 4A, 18C,D,E); *Gliricola* (Risler & Geising 1965): 2; *Myrsidea* (Buckup 1959): 6; *Pseudomenopon* (Haub 1967): 6; *Piagetiella* (ps): + (Figs. 20C,E,G); *Trochiloecetes* (Haub 1983): 2.2.2.2.; *Trimenopon* (Stöwe 1943): Abd.; *Bovicola* (Risler 1951): 5; *Ornithobius* (Haub 1971): 4.2.1.1.; *Columbicola* (ps): + (Figs. 22E,F,G); *Haematopinus* (Ramcke 1965): 11; *Hybophthirus* (Tröster 1990a): M20; *Pediculus* (ps): + (Figs. 25C,D,F); *Phthirus* (Hirsch 1986): M2; *Haematomyzus* (Weber 1969): 5; *Macroxyela* (Beutel & Vilhelmsen 2007): M.12; *Osmylus* (Beutel et al. 2010): M12; *Schizodactylus* (Khattar 1964): 8; *Oniscigaster* (Staniczek 2001): M27; *Zorotypus* (Beutel & Weide 2005): M.12; *Perla* (Chisholm 1962): M. AB. M.

0md4, M. hypopharyngomandibularis

Systelloderes (Spangenberg et al. 2013b): M12b (Fig. 4D); *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): -; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): M12b; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972)*:* -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): + (Figs. 10D, 11A); *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): -; *Psococerastis* (Masumoto & Nagashima 1993): 26; *Stenopsocus* (Badonnel 1934): O; *Caecilius* (ps): +; *Cerobasis* (ps): + (Figs. 4B, 16D); *Troctes* (Noland 1924): -; *Liposcelis* (ps): + (Figs. 4A, 18B,C); *Gliricola* (Risler & Geising 1965): 3; *Myrsidea* (Buckup 1959): 8; *Pseudomenopon* (Haub 1967): 8; *Piagetiella* (ps): + (Figs. 20B,C,E); *Trochiloecetes* (Haub 1983): 3.3.2.2.; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): 7; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): + (Figs. 22D,E); *Haematopinus* (Ramcke 1965): 12; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): + (Figs. 25C,D,E); *Phthirus* (Hirsch 1986): M3; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): 11; *Oniscigaster* (Staniczek 2001): M32; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

0md5, M. tentoriomandibularis lateralis superior

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): -; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -;

Tibicina (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): 6 (Fig. 4E); *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): -; *Psococerastis* (Masumoto & Nagashima 1993): 26; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): -; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): M28; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

0md6, M. tentoriomandibularis lateralis inferior

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): -; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): M12c (see corrected fig. 11); *Hemiodoecus* (Singh 1971): 10; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): m. retr. mand. 1+2; *Macrosiphum* (Singh 1971): 10; *Dactylosphaera* (Rilling 1960): 9; *Trialeurodes* (Weber 1935): m. retr. mand.; *Aleurolobus* (Singh 1971): 10; *Aleyrodes* (ps): +; *Psylla* (Weber 1929): m. retr. mand. (origin shifted to margin of postclypeus, which is close to the anterior tentorial arm); *Diaphorina* (Singh 1971): 10; *Cacopsylla* (ps): +; *Pseudococcus* (ps): +; *Perissopneumon* (Singh 1971): 10; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): 5 (Fig. 4E); *Philaenus* (ps): +; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): 10; *Oxyrhachis* (Singh 1971): 10; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): 10; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): 9; *Aeolothrips intermedius* (Moritz 1982b): Mandibelligament (the homology of M. tentorio-mandibularis in *Aeolothrips fasciatus* with the “Mandibelligament” connecting the mandibular base with the anterior tentorial arm in Tubulifera [Mickoleit 1963] was confirmed by Moritz [1982b]. Moritz [1982b] documented this structure in another species of the genus *Aeolothrips* showing a gradual transition from a muscle to a ligament-like structure); *Thrips* (Risler 1957): MdLig; *Haplothrips* (Mickoleit 1963): Mandibelligament; *Phlaeothrips* (Mickoleit 1963): Mandibelligament (Fig. 4C); *Psocus* (Cope 1940): -; *Psococerastis* (Masumoto & Nagashima 1993): 25; *Stenopsocus* (Badonnel 1934): P; *Caecilius* (ps): +; *Cerobasis* (ps): + (Figs. 4B, 16D); *Troctes* (Noland 1924): -; *Liposcelis* (ps): + (Figs. 4A, 18D); *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): 9+10; *Pseudomenopon* (Haub 1967): 9+10; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): 8+9; *Ornithobius* (Haub 1971): 4.2.1.3.+4.2.1.4.; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): M.13; *Osmylus* (Beutel et al. 2010): M14; *Schizodactylus* (Khattar 1964): 10; *Oniscigaster* (Staniczek 2001): M29; *Zorotypus* (Beutel & Weide 2005): M.13; *Perla* (Chisholm 1962): -

0md7, M. tentoriomandibularis medialis superior

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): -; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al.

2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): -; *Psococerastis* (Masumoto & Nagashima 1993): -; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): -; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): M30; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

0md8, M. tentoriomandibularis medialis inferior

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): -; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): 12; *Phlaeothrips* (Mickoleit 1963): 12 (Fig. 4C); *Psocus* (Cope 1940): -; *Psococerastis* (Masumoto & Nagashima 1993): -; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): + (Fig. 4B); *Troctes* (Noland 1924): -; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): M31; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

0mdx1, mandibular retractor (Hemiptera)

Systelloderes (Spangenberg et al. 2013b): M12a (Fig. 4D); *Cryptostemma* (Spangenberg et al. 2013b): M12a; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): KM11; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): KM11; *Lethocerus* (Parsons 1968): H11; *Belostoma* (Verma et al. 1973): ? (Verma et al. [1973] mentioned “protractor and retractor muscles R: MD.” originating on the head capsule, but without an adequate description); *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): M12a; *Hydrometra* (Sprague 1956): mandibular retractor; *Saldula* (Parsons 1962): 11; *Triatoma* (Barth 1952a,b, 1953a,b): Mu11; *Dysdercus* (Khan 1972): RMD2; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -;

Diaphorina (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): 4 (Fig. 4E); *Philaenus* (ps): +; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): 9; *Oxyrhachis* (Singh 1971): 9; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): 9; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): ?; *Psococerastis* (Masumoto & Nagashima 1993): ?; *Stenopsocus* (Badonnel 1934): ?; *Caecilius* (ps): ?; *Cerobasis* (ps): ?; *Troctes* (Noland 1924): ?; *Liposcelis* (ps): ?; *Gliricola* (Risler & Geising 1965): ?; *Myrsidea* (Buckup 1959): ?; *Pseudomenopon* (Haub 1967): ?; *Piagetiella* (ps): ?; *Trochiloecetes* (Haub 1983): ?; *Trimenopon* (Stöwe 1943): ?; *Bovicola* (Risler 1951): ?; *Ornithobius* (Haub 1971): ?; *Columbicola* (ps): ?; *Haematopinus* (Ramcke 1965): ?; *Hybophthirus* (Tröster 1990a): ?; *Pediculus* (ps): ?; *Phthirus* (Hirsch 1986): ?; *Haematomyzus* (Weber 1969): ?; *Macroxyela* (Beutel & Vilhelmsen 2007): ?; *Osmylus* (Beutel et al. 2010): ?; *Schizodactylus* (Khattar 1964): ?; *Oniscigaster* (Staniczek 2001): ?; *Zorotypus* (Beutel & Weide 2005): ?; *Perla* (Chisholm 1962): ?

0mdx2, mandibular retractor (Hemiptera)

Systelloderes (Spangenberg et al. 2013b): M12 (Fig. 4D); *Cryptostemma* (Spangenberg et al. 2013b): M12; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): KM10; *Corixa* (Benwitz 1956): retr. mand.; *Gelastocoris* (Parsons 1959): KM10; *Lethocerus* (Parsons 1968): H10; *Belostoma* (Verma et al. 1973): ? (see other retractors); *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): KM10; *Gerris* (Spangenberg et al. 2013b): M12; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1962): 10; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): RMD1; *Hackeriella* (Spangenberg et al. 2013a): M12; *Hemiodoecus* (Singh 1971): 7; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): 7; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): +; *Pseudococcus* (ps): + (Fig. 10D); *Perissopneumon* (Singh 1971): 7; *Tibicina* (Snodgrass 1927; Kramer 1950): rmds; *Idiocerus* (Arora & Singh 1962): 7 (Fig. 4E); *Philaenus* (ps): +; *Lepyronia* (Kramer 1950): rmds; *Platypleura* (Singh 1971): 7; *Oxyrhachis* (Singh 1971): 7; *Scolops* (Kramer 1950): rmds; *Melicharia* (Singh 1971): 7; *Dictyophara* (ps): +; *Aeolothrips fasciatus* (Mickoleit 1963): 8; *Aeolothrips intermedius* (Moritz 1982b): M.18; *Thrips* (Risler 1957): 5; *Haplothrips* (Mickoleit 1963): 8; *Phlaeothrips* (Mickoleit 1963): 8 (Fig. 4C); *Psocus* (Cope 1940): ?; *Psococerastis* (Masumoto & Nagashima 1993): ?; *Stenopsocus* (Badonnel 1934): ?; *Caecilius* (ps): ?; *Cerobasis* (ps): ?; *Troctes* (Noland 1924): ?; *Liposcelis* (ps): ?; *Gliricola* (Risler & Geising 1965): ?; *Myrsidea* (Buckup 1959): ?; *Pseudomenopon* (Haub 1967): ?; *Piagetiella* (ps): ?; *Trochiloecetes* (Haub 1983): ?; *Trimenopon* (Stöwe 1943): ?; *Bovicola* (Risler 1951): ?; *Ornithobius* (Haub 1971): ?; *Columbicola* (ps): ?; *Haematopinus* (Ramcke 1965): ?; *Hybophthirus* (Tröster 1990a): ?; *Pediculus* (ps): ?; *Phthirus* (Hirsch 1986): ?; *Haematomyzus* (Weber 1969): ?; *Macroxyela* (Beutel & Vilhelmsen 2007): ?; *Osmylus* (Beutel et al. 2010): ?; *Schizodactylus* (Khattar 1964): ?; *Oniscigaster* (Staniczek 2001): ?; *Zorotypus* (Beutel & Weide 2005): ?; *Perla* (Chisholm 1962): ?

0mdx3, protractor of mandibular lever (Hemiptera)

Systelloderes (Spangenberg et al. 2013b): M14 (Fig. 4D); *Cryptostemma* (Spangenberg et al. 2013b): M14; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): KM9; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): KM9; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): ? (see other retractors); *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): M14; *Hydrometra* (Sprague 1956): mandibular protractor; *Saldula* (Parsons 1962): 9; *Triatoma* (Barth 1952a,b, 1953a,b): Mu8; Dysdercus (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): M14 (see corrected fig. 11); *Hemiodoecus* (Singh 1971): 4; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): 4; *Dactylosphaera* (Rilling 1960): 11; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): 4; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): m. protr. mand.; *Diaphorina* (Singh 1971): 4; *Cacopsylla* (ps): +; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): 4; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): 10 (Fig. 4E); *Philaenus*

(ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): 4; *Oxyrhachis* (Singh 1971): 4; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): 4; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): ?; *Psococerastis* (Masumoto & Nagashima 1993): ?; *Stenopsocus* (Badonnel 1934): ?; *Caecilius* (ps): ?; *Cerobasis* (ps): ?; *Troctes* (Noland 1924): ?; *Liposcelis* (ps): ?; *Gliricola* (Risler & Geising 1965): ?; *Myrsidea* (Buckup 1959): ?; *Pseudomenopon* (Haub 1967): ?; *Piagetiella* (ps): ?; *Trochiloecetes* (Haub 1983): ?; *Trimenopon* (Stöwe 1943): ?; *Bovicola* (Risler 1951): ?; *Ornithobius* (Haub 1971): ?; *Columbicola* (ps): ?; *Haematopinus* (Ramcke 1965): ?; *Hybophthirus* (Tröster 1990a): ?; *Pediculus* (ps): ?; *Phthirus* (Hirsch 1986): ?; *Haematomyzus* (Weber 1969): ?; *Macroxyela* (Beutel & Vilhelmsen 2007): ?; *Osmylus* (Beutel et al. 2010): ?; *Schizodactylus* (Khattar 1964): ?; *Oniscigaster* (Staniczek 2001): ?; *Zorotypus* (Beutel & Weide 2005): ?; *Perla* (Chisholm 1962): ?

0mdx4, protractor of mandibular lever (Hemiptera)
Systelloderes (Spangenberg et al. 2013b): M13 (Fig. 4D); *Cryptostemma* (Spangenberg et al. 2013b): M13; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): KM8; *Corixa* (Benwitz 1956): protr mand; *Gelastocoris* (Parsons 1959): KM8; *Lethocerus* (Parsons 1968): H8; *Belostoma* (Verma et al. 1973): ? (see other retractors); *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): KM8; *Gerris* (Spangenberg et al. 2013b): M13; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1962): 8; *Triatoma* (Barth 1952a,b, 1953a,b): ? (the position of Mu15 is similar but it inserts on the lateral margins of the gula); *Dysdercus (*Khan 1972): PMD; *Hackeriella* (Spangenberg et al. 2013a): M13 (see corrected fig. 11); *Hemiodoecus* (Singh 1971): 5; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): m. protr. mand.; *Macrosiphum* (Singh 1971): 5; *Dactylosphaera* (Rilling 1960): 11; *Trialeurodes* (Weber 1935): m. protr. mand.; *Aleurolobus* (Singh 1971): 5; *Aleyrodes* (ps): +; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): + (Figs. 10E,F, 11A); *Perissopneumon* (Singh 1971): 5; *Tibicina* (Snodgrass 1927; Kramer 1950): pmds; *Idiocerus* (Arora & Singh 1962): 9 (homology implies shift of insertion from lever to base of stylet) (Fig. 4E); *Philaenus* (ps): +; *Lepyronia* (Kramer 1950): pmds; *Platypleura* (Singh 1971): 5; *Oxyrhachis* (Singh 1971): 5; *Scolops* (Kramer 1950): pmds; *Melicharia* (Singh 1971): 5; *Dictyophara* (ps): +; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): ?; *Psococerastis* (Masumoto & Nagashima 1993): ?; *Stenopsocus* (Badonnel 1934): ?; *Caecilius* (ps): ?; *Cerobasis* (ps): ?; *Troctes* (Noland 1924): ?; *Liposcelis* (ps): ?; *Gliricola* (Risler & Geising 1965): ?; *Myrsidea* (Buckup 1959): ?; *Pseudomenopon* (Haub 1967): ?; *Piagetiella* (ps): ?; *Trochiloecetes* (Haub 1983): ?; *Trimenopon* (Stöwe 1943): ?; *Bovicola* (Risler 1951): ?; *Ornithobius* (Haub 1971): ?; *Columbicola* (ps): ?; *Haematopinus* (Ramcke 1965): ?; *Hybophthirus* (Tröster 1990a): ?; *Pediculus* (ps): ?; *Phthirus* (Hirsch 1986): ?; *Haematomyzus* (Weber 1969): ?; *Macroxyela* (Beutel & Vilhelmsen 2007): ?; *Osmylus* (Beutel et al. 2010): ?; *Schizodactylus* (Khattar 1964): ?; *Oniscigaster* (Staniczek 2001): ?; *Zorotypus* (Beutel & Weide 2005): ?; *Perla* (Chisholm 1962): ?

0mdx5, protractor of mandible (Hemiptera)
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): ? (see other retractors); *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): 6 (see corrected fig. 11); *Hemiodoecus* (Singh 1971): 6; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): ? (m. lam. mand1 + 2 are similar in position, but restricted to the cranial skeletal structures “Seitenapodem” with postclypeal origin and lorum); *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): m. add. mand.; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): +; *Pseudococcus* (ps): + (Figs. 10D, 11A); *Perissopneumon* (Singh 1971): 6;

Tibicina (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): 8 (Fig. 4E); *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): 6; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): ?; *Psococerastis* (Masumoto & Nagashima 1993): ?; *Stenopsocus* (Badonnel 1934): ?; *Caecilius* (ps): ?; *Cerobasis* (ps): ?; *Troctes* (Noland 1924): ?; *Liposcelis* (ps): ?; *Gliricola* (Risler & Geising 1965): ?; *Myrsidea* (Buckup 1959): ?; *Pseudomenopon* (Haub 1967): ?; *Piagetiella* (ps): ?; *Trochiloecetes* (Haub 1983): ?; *Trimenopon* (Stöwe 1943): ?; *Bovicola* (Risler 1951): ?; *Ornithobius* (Haub 1971): ?; *Columbicola* (ps): ?; *Haematopinus* (Ramcke 1965): ?; *Hybophthirus* (Tröster 1990a): ?; *Pediculus* (ps): ?; *Phthirus* (Hirsch 1986): ?; *Haematomyzus* (Weber 1969): ?; *Macroxyela* (Beutel & Vilhelmsen 2007): ?; *Osmylus* (Beutel et al. 2010): ?; *Schizodactylus* (Khattar 1964): ?; *Oniscigaster* (Staniczek 2001): ?; *Zorotypus* (Beutel & Weide 2005): ?; *Perla* (Chisholm 1962): ?

0mdx6, retractor of mandible (Hemiptera)
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): ? (see other retractors); *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): 8; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): ?; *Psococerastis* (Masumoto & Nagashima 1993): ?; *Stenopsocus* (Badonnel 1934): ?; *Caecilius* (ps): ?; *Cerobasis* (ps): ?; *Troctes* (Noland 1924): ?; *Liposcelis* (ps): ?; *Gliricola* (Risler & Geising 1965): ?; *Myrsidea* (Buckup 1959): ?; *Pseudomenopon* (Haub 1967): ?; *Piagetiella* (ps): ?; *Trochiloecetes* (Haub 1983): ?; *Trimenopon* (Stöwe 1943): ?; *Bovicola* (Risler 1951): ?; *Ornithobius* (Haub 1971): ?; *Columbicola* (ps): ?; *Haematopinus* (Ramcke 1965): ?; *Hybophthirus* (Tröster 1990a): ?; *Pediculus* (ps): ?; *Phthirus* (Hirsch 1986): ?; *Haematomyzus* (Weber 1969): ?; *Macroxyela* (Beutel & Vilhelmsen 2007): ?; *Osmylus* (Beutel et al. 2010): ?; *Schizodactylus* (Khattar 1964): ?; *Oniscigaster* (Staniczek 2001): ?; *Zorotypus* (Beutel & Weide 2005): ?; *Perla* (Chisholm 1962): ?

0mdx7, retractor of mandible (Hemiptera)
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): -; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): 10; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -;

Phlaeothrips (Mickoleit 1963): -; *Psocus* (Cope 1940): ?; *Psococerastis* (Masumoto & Nagashima 1993): ?; *Stenopsocus* (Badonnel 1934): ?; *Caecilius* (ps): ?; *Cerobasis* (ps): ?; *Troctes* (Noland 1924): ?; *Liposcelis* (ps): ?; *Gliricola* (Risler & Geising 1965): ?; *Myrsidea* (Buckup 1959): ?; *Pseudomenopon* (Haub 1967): ?; *Piagetiella* (ps): ?; *Trochiloecetes* (Haub 1983): ?; *Trimenopon* (Stöwe 1943): ?; *Bovicola* (Risler 1951): ?; *Ornithobius* (Haub 1971): ?; *Columbicola* (ps): ?; *Haematopinus* (Ramcke 1965): ?; *Hybophthirus* (Tröster 1990a): ?; *Pediculus* (ps): ?; *Phthirus* (Hirsch 1986): ?; *Haematomyzus* (Weber 1969): ?; *Macroxyela* (Beutel & Vilhelmsen 2007): ?; *Osmylus* (Beutel et al. 2010): ?; *Schizodactylus* (Khattar 1964): ?; *Oniscigaster* (Staniczek 2001): ?; *Zorotypus* (Beutel & Weide 2005): ?; *Perla* (Chisholm 1962): ?

Muscles of the maxillae

0mx1, M. craniocardinalis

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): -; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): anterior dorsal muscle; *Psococerastis* (Masumoto & Nagashima 1993): -; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): -; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): M.15; *Osmylus* (Beutel et al. 2010): M15; *Schizodactylus* (Khattar 1964): 12; *Oniscigaster* (Staniczek 2001): M34; *Zorotypus* (Beutel & Weide 2005): M.15; *Perla* (Chisholm 1962): PR. CAR.

0mx2, M. craniolacinialis

Systelloderes (Spangenberg et al. 2013b): M15; *Cryptostemma* (Spangenberg et al. 2013b): M15; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): KM13; *Corixa* (Benwitz 1956): retr max; *Gelastocoris* (Parsons 1959): KM13; *Lethocerus* (Parsons 1968): H13; *Belostoma* (Verma et al. 1973): R. MX.; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): KM13; *Gerris* (Spangenberg et al. 2013b): M15; *Hydrometra* (Sprague 1956): maxillary retractor; *Saldula* (Parsons 1962): 13; *Triatoma* (Barth 1952a,b, 1953a,b): Mu9 + Mu10 (see also interpretation in Rieger 1976); *Dysdercus* (Khan 1972): RMX; *Hackeriella* (Spangenberg et al. 2013a): M15; *Hemiodoecus* (Singh 1971): 13; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): m. retr. max1 + 2 (see also interpretation in Rieger 1976); *Macrosiphum* (Singh 1971): 13; *Dactylosphaera* (Rilling 1960): 12; *Trialeurodes* (Weber 1935): m. retr. max2 (see also Fig. 5E); *Aleurolobus* (Singh 1971): 13; *Aleyrodes* (ps): +; *Psylla* (Weber 1929): m. retr. max.; *Diaphorina* (Singh 1971): 13; *Cacopsylla* (ps): +; *Pseudococcus* (ps): + (Fig. 10E); *Perissopneumon* (Singh 1971): 13; *Tibicina* (Snodgrass 1927; Kramer 1950): rmxs1+2 (Fig. 5D); *Idiocerus* (Arora & Singh 1962): 11; *Philaenus* (ps): +; *Lepyronia* (Kramer 1950): rmxs; *Platypleura* (Singh 1971): 13; *Oxyrhachis* (Singh 1971): 13; *Scolops* (Kramer 1950): rmxs; *Melicharia* (Singh 1971): 13; *Dictyophara* (ps): +; *Aeolothrips fasciatus* (Mickoleit 1963): 15 (Fig. 5C); *Aeolothrips*

intermedius (Moritz 1982b): M.22 (Fig. 5C); *Thrips* (Risler 1957): 6; *Haplothrips* (Mickoleit 1963): 15; *Phlaeothrips* (Mickoleit 1963): 15; *Psocus* (Cope 1940): cranial flexor of lacinia; *Psococerastis* (Masumoto & Nagashima 1993): 5; *Stenopsocus* (Badonnel 1934): R1; *Caecilius* (ps): +; *Cerobasis* (ps): + (Figs. 5A, 16E); *Troctes* (Noland 1924): r. f.; *Liposcelis* (ps): + (Fig. 18J); *Gliricola* (Risler & Geising 1965): 8; *Myrsidea* (Buckup 1959): 16; *Pseudomenopon* (Haub 1967): 16 (Fig. 5B); *Piagetiella* (ps): + (Fig. 20G); *Trochiloecetes* (Haub 1983): 2.3.2.7.; *Trimenopon* (Stöwe 1943): ? (As outlined in the main body of the text the “lacinia” of Stöwe (1943) is presumably the galea. Consequently, the homology of the musculature in Stöwe (1943) is questionable); *Bovicola* (Risler 1951): 11; *Ornithobius* (Haub 1971): 4.3.1.3.; *Columbicola* (ps): + (Fig. 22G); *Haematopinus* (Ramcke 1965): 13; *Hybophthirus* (Tröster 1990a): M22; *Pediculus* (ps): + (Fig. 25F); *Phthirus* (Hirsch 1986): M5; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): M.19; *Osmylus* (Beutel et al. 2010): M19; *Schizodactylus* (Khattar 1964): 15; *Oniscigaster* (Staniczek 2001): M35; *Zorotypus* (Beutel & Weide 2005): M.19; *Perla* (Chisholm 1962): CR. F. L.

0mx3, M. tentoriocardinalis

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): -; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): 16 (Fig. 5C); *Aeolothrips intermedius* (Moritz 1982b): M.23 (Fig. 5C); *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): -; *Psococerastis* (Masumoto & Nagashima 1993): -; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): -; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): M.17; *Osmylus* (Beutel et al. 2010): M17; *Schizodactylus* (Khattar 1964): 13a+13b; *Oniscigaster* (Staniczek 2001): M33; *Zorotypus* (Beutel & Weide 2005): M.17; *Perla* (Chisholm 1962): CAR. AD. M.

0mx4, M. tentoriostipitalis anterior

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): -; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -;

Phlaeothrips (Mickoleit 1963): -; *Psocus* (Cope 1940): -; *Psococerastis* (Masumoto & Nagashima 1993): -; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): -; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): 14; *Oniscigaster* (Staniczek 2001): M37+M38; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): ST. AD. M.

0mx5, M. tentoriostipitalis posterior

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): -; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): ventral adductor muscles; *Psococerastis* (Masumoto & Nagashima 1993): 4; *Stenopsocus* (Badonnel 1934): R; *Caecilius* (ps): +; *Cerobasis* (ps): + (Figs. 5A, 16E,F); *Troctes* (Noland 1924): -; *Liposcelis* (ps): + (Figs. 18G,H); *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): 11; *Pseudomenopon* (Haub 1967): 11 (Fig. 5B); *Piagetiella* (ps): + (Fig. 20F); *Trochiloecetes* (Haub 1983): 2.3.2.1.; *Trimenopon* (Stöwe 1943): M1; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): 4.3.1.2.; *Columbicola* (ps): + (Fig. 22F); *Haematopinus* (Ramcke 1965): 14; *Hybophthirus* (Tröster 1990a): M24; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): M.18; *Osmylus* (Beutel et al. 2010): M18; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): M36; *Zorotypus* (Beutel & Weide 2005): M.18; *Perla* (Chisholm 1962): ST. AD. M.

0mx6, M. stipitolacinialis

Systelloderes (Spangenberg et al. 2013b): M16; *Cryptostemma* (Spangenberg et al. 2013b): M16; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): KM12; *Corixa* (Benwitz 1956): protr max; *Gelastocoris* (Parsons 1959): KM12; *Lethocerus* (Parsons 1968): H12; *Belostoma* (Verma et al. 1973): P. MX.; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): KM12; *Gerris* (Spangenberg et al. 2013b): M16; *Hydrometra* (Sprague 1956): +; *Saldula* (Parsons 1962): 12; *Triatoma* (Barth 1952a,b, 1953a,b): Mu6 + Mu7; *Dysdercus* (Khan 1972): PMX1+2; *Hackeriella* (Spangenberg et al. 2013a): M16; *Hemiodoecus* (Singh 1971): 11; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): m. protr. max1–3; *Macrosiphum* (Singh 1971): 11; *Dactylosphaera* (Rilling 1960): 14; *Trialeurodes* (Weber 1935): m. protr. max. (see also Fig. 5E); *Aleurolobus* (Singh 1971): 11; *Aleyrodes* (ps): +; *Psylla* (Weber 1929): m. protr. max.; *Diaphorina* (Singh 1971): 11; *Cacopsylla* (ps): +; *Pseudococcus* (ps): + (Figs. 11B,C); *Perissopneumon* (Singh 1971): 11; *Tibicina* (Snodgrass 1927; Kramer 1950): pmxs (Fig. 5D); *Idiocerus* (Arora & Singh 1962): 12; *Philaenus* (ps): +; *Lepyronia* (Kramer 1950): pmxs; *Platypleura* (Singh 1971): 11; *Oxyrhachis* (Singh 1971): 11; *Scolops* (Kramer 1950): pmxs; *Melicharia* (Singh 1971): 11; *Dictyophara* (ps): +; *Aeolothrips fasciatus* (Mickoleit 1963): ?; *Aeolothrips intermedius* (Moritz 1982b): ?; *Thrips* (Risler 1957): ?; *Haplothrips* (Mickoleit 1963): ?; *Phlaeothrips* (Mickoleit 1963): ?; *Psocus* (Cope 1940): stipital flexor of lacinia; *Psococerastis* (Masumoto & Nagashima 1993):

6; *Stenopsocus* (Badonnel 1934): Lp1–3; *Caecilius* (ps): +; *Cerobasis* (ps): + (Figs. 5A, 16E,F); *Troctes* (Noland 1924): f. m.; *Liposcelis* (ps): + (Figs. 18F,G,H); *Gliricola* (Risler & Geising 1965): 9; *Myrsidea* (Buckup 1959): 17; *Pseudomenopon* (Haub 1967): 17 (Fig. 5B); *Piagetiella* (ps): + (Fig. 20F); *Trochiloecetes* (Haub 1983): 2.3.2.6.; *Trimenopon* (Stöwe 1943): ? (see **0mx2, M. craniolacinialis**); *Bovicola* (Risler 1951): 12; *Ornithobius* (Haub 1971): 4.3.1.4.; *Columbicola* (ps): +; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): M21; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): M.20; *Osmylus* (Beutel et al. 2010): M20; *Schizodactylus* (Khattar 1964): 16; *Oniscigaster* (Staniczek 2001): M39; *Zorotypus* (Beutel & Weide 2005): M.20; *Perla* (Chisholm 1962): ST. F. L.

0mx7, M. stipitogalealis

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): -; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -.; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): -; *Psococerastis* (Masumoto & Nagashima 1993): -; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): + (Figs. 5A, 16F,G); *Troctes* (Noland 1924): g. m. e.; *Liposcelis* (ps): + (Figs. 18F,G,H); *Gliricola* (Risler & Geising 1965): 7; *Myrsidea* (Buckup 1959): 15; *Pseudomenopon* (Haub 1967): 15 (Fig. 5B); *Piagetiella* (ps): +; *Trochiloecetes* (Haub 1983): 2.3.2.2.; *Trimenopon* (Stöwe 1943): M2 (As outlined in the main body of the text the “lacinia” of Stöwe (1943) is presumably the galea *sensu stricto*); *Bovicola* (Risler 1951): 10; *Ornithobius* (Haub 1971): 4.3.1.1.; *Columbicola* (ps): + (Fig. 22F); *Haematopinus* (Ramcke 1965): 15; *Hybophthirus* (Tröster 1990a): M23; *Pediculus* (ps): + (Fig. 25E); *Phthirus* (Hirsch 1986): M4; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): M.21; *Osmylus* (Beutel et al. 2010): M21; *Schizodactylus* (Khattar 1964): 17; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): M.21; *Perla* (Chisholm 1962): galeal abductor muscle

0mx8, M. stipitopalpalis externus

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): -; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -.; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): 17 (Fig. 5C); *Aeolothrips intermedius* (Moritz 1982b): M.24 (Fig. 5C); *Thrips* (Risler 1957): 9; *Haplothrips* (Mickoleit 1963): 17; *Phlaeothrips* (Mickoleit 1963): 17; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): 10; *Stenopsocus* (Badonnel 1934): m1; *Caecilius* (ps): +; *Cerobasis* (ps): +

(Figs. 5A, 16F,G); *Troctes* (Noland 1924): f. p.; *Liposcelis* (ps): + (Figs. 18F,G); *Gliricola* (Risler & Geising 1965): 4; *Myrsidea* (Buckup 1959): 12; *Pseudomenopon* (Haub 1967): 12 (Fig. 5B); *Piagetiella* (ps): + (Fig. 20F); *Trochiloecetes* (Haub 1983): 2.3.2.3.; *Trimenopon* (Stöwe 1943): m1; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): M.22; *Osmylus* (Beutel et al. 2010): M22; *Schizodactylus* (Khattar 1964): 18; *Oniscigaster* (Staniczek 2001): M40; *Zorotypus* (Beutel & Weide 2005): M.22; *Perla* (Chisholm 1962): L. MX. P.

0mx9, M. stipitopalpalis medialis

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): -; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -.; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): 18 (Fig. 5C); *Aeolothrips intermedius* (Moritz 1982b): M.25 (Fig. 5C); *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): -; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): e. p.; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): M.23; *Osmylus* (Beutel et al. 2010): M23; *Schizodactylus* (Khattar 1964): 19; *Oniscigaster* (Staniczek 2001): M41; *Zorotypus* (Beutel & Weide 2005): M.23; *Perla* (Chisholm 1962): D. MX. P.

0mx10, M. stipitopalpalis internus

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): -; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -.; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): 9; *Stenopsocus* (Badonnel 1934): m2; *Caecilius* (ps): +; *Cerobasis* (ps): + (Fig. 5A); *Troctes* (Noland 1924): ? (muscle of the second maxillary palpomere, homologization impeded by the missing description); *Liposcelis* (ps): + (Fig. 18D); *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon*

(Stöwe 1943): m2; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

0mx11, M. stipitalis transversalis
absent in all taxa examined and not mentioned in other studies

0mx12, M. palpopalpalis maxillae primus
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): -; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -.; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): m'2; *Caecilius* (ps): +; *Cerobasis* (ps): + (Fig. 5A); *Troctes* (Noland 1924): ? (muscle of the second maxillary palpomere, homologization impeded by the missing description); *Liposcelis* (ps): +; *Gliricola* (Risler & Geising 1965): 5 (This interpretation differs from Haub [1967], who homologized muscle 6 of *Gliricola* with muscle 14 of *Trimenopon*, even though the latter originates on the second palpomere whereas this is the insertion of the former.); *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): M.24; *Osmylus* (Beutel et al. 2010): M24; *Schizodactylus* (Khattar 1964): 20; *Oniscigaster* (Staniczek 2001): M42; *Zorotypus* (Beutel & Weide 2005): M.24; *Perla* (Chisholm 1962): flexor muscle in the first palpomere

0mx13, M. palpopalpalis maxillae secundus
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): -; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -.; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): m3; *Caecilius* (ps): +; *Cerobasis* (ps): + (Figs. 5A, 16D);

Troctes (Noland 1924): /; *Liposcelis* (ps): + (Fig. 18C); *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): second partition of 14; *Pseudomenopon* (Haub 1967): 14 (Fig. 5B); *Piagetiella* (ps): +; *Trochiloecetes* (Haub 1983): 2.3.2.5.; *Trimenopon* (Stöwe 1943): m5; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): M.25 + M.26; *Osmylus* (Beutel et al. 2010): M25; *Schizodactylus* (Khattar 1964): 21; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): M.25; *Perla* (Chisholm 1962): flexor muscle in the second palpomere

0mx14, M. palpopalpalis maxillae tertius

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): -; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -.; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): m3 (In *Cerobasis* 0mx13 inserts at the base of the third palpomere. 0mx14 originates just anterad this insertion and then bends towards the base of the fourth palpomere. This condition is very similiar to that of m3 of Badonnel [1934], which suggests that Badonnel's m3 is in fact 0mx13 and 0mx14 [but see similar condition in Haub 1967, muscle 13. and 14.]. Two internal maxillary palpal muscles are also present in *Myrsidea* [Buckup 1959]. In contrast to the condition found in *Cerobasis* the second partition of 14. Musc. palpi maxillaris secundus of *Myrsidea* does not insert on the border region of the second and third maxillary palpomere, but on the border region of the third and fourth palpomere [Buckup 1959], which is similar to the condition of m3 of *Stenopsocus* [Badonnel 1934]. This also suggests that 0mx13 and 0mx14 may be fused to a single muscle.); *Caecilius* (ps): +; *Cerobasis* (ps): + (Fig. 5A); *Troctes* (Noland 1924): /; *Liposcelis* (ps): +; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): first partition of 14; *Pseudomenopon* (Haub 1967): 14 (similar condidition as described in Badonnel [1934]) (Fig. 5B); *Piagetiella* (ps): + (similar condidition as described in Badonnel [1934]); *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): m4; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): M26; *Schizodactylus* (Khattar 1964): 22; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): M.26; *Perla* (Chisholm 1962): flexor muscle in the third palpomere

0mx15, M. palpopalpalis maxillae quartus

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): -; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -.; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -;

Diaphorina (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): M.27; *Osmylus* (Beutel et al. 2010): M27; *Schizodactylus* (Khattar 1964): 23; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): M.27; *Perla* (Chisholm 1962): flexor muscle in the fourth palpomere

0mxx1, "M. craniolacinialis secundus"
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): -; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -.; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): -; *Psococerastis* (Masumoto & Nagashima 1993): -; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): + (Figs. 5A, 16E); *Troctes* (Noland 1924): -; *Liposcelis* (ps): + (Fig. 18I); *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

0mxx2, "M. palpopalpalis maxillae secundus secundus"
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): -; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -.; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -;

Aeolothrips intermedius (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): -; *Psococerastis* (Masumoto & Nagashima 1993): -; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): -; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): 13 (Fig. 5B); *Piagetiella* (ps): +; *Trochiloecetes* (Haub 1983): 2.3.2.4.; *Trimenopon* (Stöwe 1943): m3; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

0mxx3, retractor of maxillary lever

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): -; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): 13; *Trialeurodes* (Weber 1935): m. retr. max3. (see also Fig. 5E); *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): +; *Pseudococcus* (ps): + (Figs. 11B,C); *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): rmxl (Fig. 5D); *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): +; *Lepyronia* (Kramer 1950): rmxl; *Platypleura* (Singh 1971): 14; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): 14 (Fig. 5C); *Aeolothrips intermedius* (Moritz 1982b): M.21 (Fig. 5C); *Thrips* (Risler 1957): 7; *Haplothrips* (Mickoleit 1963): 14; *Phlaeothrips* (Mickoleit 1963): 14; *Psocus* (Cope 1940): ?; *Psococerastis* (Masumoto & Nagashima 1993): ?; *Stenopsocus* (Badonnel 1934): ?; *Caecilius* (ps): ?; *Cerobasis* (ps): ?; *Troctes* (Noland 1924): ?; *Liposcelis* (ps): ?; *Gliricola* (Risler & Geising 1965): ?; *Myrsidea* (Buckup 1959): ?; *Pseudomenopon* (Haub 1967): ?; *Piagetiella* (ps): ?; *Trochiloecetes* (Haub 1983): ?; *Trimenopon* (Stöwe 1943): ?; *Bovicola* (Risler 1951): ?; *Ornithobius* (Haub 1971): ?; *Columbicola* (ps): ?; *Haematopinus* (Ramcke 1965): ?; *Hybophthirus* (Tröster 1990a): ?; *Pediculus* (ps): ?; *Phthirus* (Hirsch 1986): ?; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): ?; *Osmylus* (Beutel et al. 2010): ?; *Schizodactylus* (Khattar 1964): ?; *Oniscigaster* (Staniczek 2001): ?; *Zorotypus* (Beutel & Weide 2005): ?; *Perla* (Chisholm 1962): ?

0mxx4, "M. lacinio-mandibularis"

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): -; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): 13; *Trialeurodes* (Weber 1935): m. retr. max3.; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): 10 (Fig. 5C); *Aeolothrips intermedius* (Moritz 1982b): M.19 (Fig. 5C); *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): -; *Psococerastis* (Masumoto & Nagashima 1993): -; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -;

Cerobasis (ps): -; *Troctes* (Noland 1924): -; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

0mxx5, protractor of maxillary lever

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): -; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): 12; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -.; *Aleurolobus* (Singh 1971): 12; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): 12; *Cacopsylla* (ps): -; *Pseudococcus* (ps): + (Figs. 10F, 11A,B); *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): pmxl (Fig. 5D); *Idiocerus* (Arora & Singh 1962): 13; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): pmxl; *Platypleura* (Singh 1971): 12; *Oxyrhachis* (Singh 1971): 12; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): 13 (Fig. 5C); *Aeolothrips intermedius* (Moritz 1982b): M.20 (Fig. 5C); *Thrips* (Risler 1957): 8; *Haplothrips* (Mickoleit 1963): 13; *Phlaeothrips* (Mickoleit 1963): 13; *Psocus* (Cope 1940): ?; *Psococerastis* (Masumoto & Nagashima 1993): ?; *Stenopsocus* (Badonnel 1934): ?; *Caecilius* (ps): ?; *Cerobasis* (ps): ?; *Troctes* (Noland 1924): ?; *Liposcelis* (ps): ?; *Gliricola* (Risler & Geising 1965): ?; *Myrsidea* (Buckup 1959): ?; *Pseudomenopon* (Haub 1967): ?; *Piagetiella* (ps): ?; *Trochiloecetes* (Haub 1983): ?; *Trimenopon* (Stöwe 1943): ?; *Bovicola* (Risler 1951): ?; *Ornithobius* (Haub 1971): ?; *Columbicola* (ps): ?; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): ?; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): ?; *Osmylus* (Beutel et al. 2010): ?; *Schizodactylus* (Khattar 1964): ?; *Oniscigaster* (Staniczek 2001): ?; *Zorotypus* (Beutel & Weide 2005): ?; *Perla* (Chisholm 1962): ?

0mxx6, "M. tentorio-lacinialis"

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): -; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): m. retr. max1 (see also Fig. 5E); *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): +; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): -; *Psococerastis* (Masumoto & Nagashima 1993): -; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): -; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -;

Haematopinus (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

0mxx7, muscle operating the maxillary gland

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): KM24; *Corixa* (Benwitz 1956): Ömu; *Gelastocoris* (Parsons 1959): KM24; *Lethocerus* (Parsons 1968): H24; *Belostoma* (Verma et al. 1973): -; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): /; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): M5a; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): /; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): /; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

0mxx8, "M. palpopalpalis maxillae primus secundus"

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): -; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): 6; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): M43; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

0mxx9, "M. stipitogalealis secundus"
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): -; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): g. m. f.; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): flexor of galea.

Muscles of the labium

0la1, M. postoccipitoglossalis medialis
absent in all taxa examined and not mentioned in other studies

0la2, M. postoccipitoglossalis lateralis
Systelloderes (Spangenberg et al. 2013b): ?; *Cryptostemma* (Spangenberg et al. 2013b): ?; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): ?; *Corixa* (Benwitz 1956): ?; *Gelastocoris* (Parsons 1959): ?; *Lethocerus* (Parsons 1968): ?; *Belostoma* (Verma et al. 1973): ?; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): ?; *Gerris* (Spangenberg et al. 2013b): ?; *Hydrometra* (Sprague 1956): ?; *Saldula* (Parsons 1962): ?; *Triatoma* (Barth 1952a,b, 1953a,b): ?; *Dysdercus* (Khan 1972): ?; *Hackeriella* (Spangenberg et al. 2013a): ?; *Hemiodoecus* (Singh 1971): ?; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): ?; *Macrosiphum* (Singh 1971): ?; *Dactylosphaera* (Rilling 1960): ?; *Trialeurodes* (Weber 1935): ?; *Aleurolobus* (Singh 1971): ?; *Aleyrodes* (ps): ?; *Psylla* (Weber 1929): ?; *Diaphorina* (Singh 1971): ?; *Cacopsylla* (ps): ?; *Pseudococcus* (ps): ?; *Perissopneumon* (Singh 1971): ?; *Tibicina* (Snodgrass 1927; Kramer 1950): ?; *Idiocerus* (Arora & Singh 1962): ?; *Philaenus* (ps): ?; *Lepyronia* (Kramer 1950): ?; *Platypleura* (Singh 1971): ?; *Oxyrhachis* (Singh 1971): ?; *Scolops* (Kramer 1950): ?; *Melicharia* (Singh 1971): ?; *Dictyophara* (ps): ?; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): D.R.L.

0la3, M. postoccipitoparaglossalis
absent in all taxa examined and not mentioned in other studies

0la4, M. postoccipitopraementalis primus
Systelloderes (Spangenberg et al. 2013b): ?; *Cryptostemma* (Spangenberg et al. 2013b): ?; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): ?; *Corixa* (Benwitz 1956): ?; *Gelastocoris* (Parsons 1959): ?; *Lethocerus* (Parsons 1968): ?; *Belostoma* (Verma et al. 1973): ?; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): ?; *Gerris* (Spangenberg et al. 2013b): ?; *Hydrometra* (Sprague 1956): ?; *Saldula* (Parsons 1962): ?; *Triatoma* (Barth 1952a,b, 1953a,b): ?; *Dysdercus* (Khan 1972): ?; *Hackeriella* (Spangenberg et al. 2013a): ?; *Hemiodoecus* (Singh 1971): ?; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): ?; *Macrosiphum* (Singh 1971): ?; *Dactylosphaera* (Rilling 1960): ?; *Trialeurodes* (Weber 1935): ?; *Aleurolobus* (Singh 1971): ?; *Aleyrodes* (ps): ?; *Psylla* (Weber 1929): ?; *Diaphorina* (Singh 1971): ?; *Cacopsylla* (ps): ?; *Pseudococcus* (ps): ?; *Perissopneumon* (Singh 1971): ?; *Tibicina* (Snodgrass 1927; Kramer 1950): ?; *Idiocerus* (Arora & Singh 1962): ?; *Philaenus* (ps): ?; *Lepyronia* (Kramer 1950): ?; *Platypleura* (Singh 1971): ?; *Oxyrhachis* (Singh 1971): ?; *Scolops* (Kramer 1950): ?; *Melicharia* (Singh 1971): ?; *Dictyophara* (ps): ?; *Aeolothrips fasciatus* (Mickoleit 1963): 19a (Fig. 6B); *Aeolothrips intermedius* (Moritz 1982b): M.26b (Fig. 6B); *Thrips* (Risler 1957): 10; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): 24; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

0la4, M. postoccipitopraementalis secundus
Systelloderes (Spangenberg et al. 2013b): ?; *Cryptostemma* (Spangenberg et al. 2013b): ?; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): ?; *Corixa* (Benwitz 1956): ?; *Gelastocoris* (Parsons 1959): ?; *Lethocerus* (Parsons 1968): ?; *Belostoma* (Verma et al. 1973): ?; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): ?; *Gerris* (Spangenberg et al. 2013b): ?; *Hydrometra* (Sprague 1956): ?; *Saldula* (Parsons 1962): ?; *Triatoma* (Barth 1952a,b, 1953a,b): ?; *Dysdercus* (Khan 1972): ?; *Hackeriella* (Spangenberg et al. 2013a): ?; *Hemiodoecus* (Singh 1971): ?; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): ?; *Macrosiphum* (Singh 1971): ?; *Dactylosphaera* (Rilling 1960): ?; *Trialeurodes* (Weber 1935): ?; *Aleurolobus* (Singh 1971): ?; *Aleyrodes* (ps): ?; *Psylla* (Weber 1929): ?; *Diaphorina* (Singh 1971): ?; *Cacopsylla* (ps): ?; *Pseudococcus* (ps): ?; *Perissopneumon* (Singh 1971): ?; *Tibicina* (Snodgrass 1927; Kramer 1950): ?; *Idiocerus* (Arora & Singh 1962): ?; *Philaenus* (ps): ?; *Lepyronia* (Kramer 1950): ?; *Platypleura* (Singh 1971): ?; *Oxyrhachis* (Singh 1971): ?; *Scolops* (Kramer 1950): ?; *Melicharia* (Singh 1971): ?; *Dictyophara* (ps): ?; *Aeolothrips fasciatus* (Mickoleit 1963): 19b; *Aeolothrips intermedius* (Moritz 1982b): M.26a; *Thrips* (Risler 1957): 18; *Haplothrips* (Mickoleit 1963): 19b; *Phlaeothrips* (Mickoleit 1963): 19b; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

0la5, M. tentoriopraementalis
Systelloderes (Spangenberg et al. 2013b): ?; *Cryptostemma* (Spangenberg et al. 2013b): ?; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): ?; *Corixa* (Benwitz 1956): ?; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): ?; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): ?; *Gerris* (Spangenberg et al. 2013b): ?; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): ?; *Triatoma* (Barth 1952a,b, 1953a,b): ?; *Dysdercus* (Khan 1972): ?; *Hackeriella* (Spangenberg et al. 2013a): ?; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): ?; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): ?; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): ?; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): ?; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): ?; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): ?; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): o (Fig. 6A); *Caecilius* (ps): +; *Cerobasis* (ps): + (Figs. 16F,G); *Troctes* (Noland 1924): /; *Liposcelis* (ps): + (Figs. 18G,H,I); *Gliricola* (Risler & Geising 1965): 14; *Myrsidea* (Buckup 1959): 20; *Pseudomenopon* (Haub 1967): 20; *Piagetiella* (ps): + (Figs. 20F,G); *Trochiloecetes* (Haub 1983): 2.4.2.4.; *Trimenopon* (Stöwe 1943): o; *Bovicola* (Risler 1951): 15; *Ornithobius* (Haub 1971): 4.4.1.3.; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): 21 (Fig. 6D); *Hybophthirus* (Tröster 1990a): M27; *Pediculus* (ps): + (Figs. 25G,H); *Phthirus* (Hirsch 1986): M8; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): M.29 + M.30; *Osmylus* (Beutel et al. 2010): M29; *Schizodactylus* (Khattar 1964): 25; *Oniscigaster* (Staniczek 2001): M46 + M47; *Zorotypus* (Beutel & Weide 2005): M29 + M30; *Perla* (Chisholm 1962): PR. R. L.

0la6, M. tentorioparaglossalis
absent in all polyneopteran and phthiraptera taxa examined, homology to 0lax1 of Hemiptera (see above) unclear

0la7, M. tentorioglandularis
absent in all taxa examined and not mentioned in other studies

0la8, M. submentopraementalis
Systelloderes (Spangenberg et al. 2013b): ?; *Cryptostemma* (Spangenberg et al. 2013b): ?; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): ?; *Corixa* (Benwitz 1956): ?; *Gelastocoris* (Parsons 1959): ?; *Lethocerus* (Parsons 1968): ?; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): ?; *Gerris* (Spangenberg et al. 2013b): ?; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): ?; *Triatoma* (Barth 1952a,b, 1953a,b): ?; *Dysdercus* (Khan 1972): ?; *Hackeriella* (Spangenberg et al. 2013a): ?; *Hemiodoecus* (Singh 1971): ?; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): ?; *Macrosiphum* (Singh 1971): ?; *Dactylosphaera* (Rilling 1960): ?; *Trialeurodes* (Weber 1935): ?; *Aleurolobus* (Singh 1971): ?; *Aleyrodes* (ps): ?; *Psylla* (Weber 1929): ?; *Diaphorina* (Singh 1971): ?; *Cacopsylla* (ps): ?; *Pseudococcus* (ps): ?; *Perissopneumon* (Singh 1971): ?; *Tibicina* (Snodgrass 1927; Kramer 1950): ?; *Idiocerus* (Arora & Singh 1962): ?; *Philaenus* (ps): ?; *Lepyronia* (Kramer 1950): ?; *Platypleura* (Singh 1971): ?; *Oxyrhachis* (Singh 1971): ?; *Scolops* (Kramer 1950): ?; *Melicharia* (Singh 1971): ?; *Dictyophara* (ps): ?; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): p (Fig. 6A); *Caecilius* (ps): +; *Cerobasis* (ps): + (Fig. 16H); *Troctes* (Noland 1924): /; *Liposcelis* (ps): + (Fig. 18H); *Gliricola* (Risler & Geising 1965): 13; *Myrsidea* (Buckup 1959): 18 + 19; *Pseudomenopon* (Haub 1967): 18 + 19; *Piagetiella* (ps): + (Figs. 20F,G,H); *Trochiloecetes* (Haub 1983): 2.4.2.1.; *Trimenopon* (Stöwe 1943): p; *Bovicola* (Risler 1951): 13; *Ornithobius* (Haub 1971): 4.4.1.1. + 4.4.1.2.; *Columbicola* (ps): + (Figs. 22F,G); *Haematopinus*

(Ramcke 1965): 20 (Fig. 6D); *Hybophthirus* (Tröster 1990a): M26; *Pediculus* (ps): + (Figs. 25G,H); *Phthirus* (Hirsch 1986): M7; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): M.28; *Osmylus* (Beutel et al. 2010): M28; *Schizodactylus* (Khattar 1964): 26; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): M.28; *Perla* (Chisholm 1962): M. R. M.

0la9, M. postmentomembranus
absent in all taxa examined and not mentioned in other studies

0la10, M. submentomentalis
absent in all taxa examined and not mentioned in other studies

0la11, M. praementoparaglossalis
Systelloderes (Spangenberg et al. 2013b): ?; *Cryptostemma* (Spangenberg et al. 2013b): ?; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): ?; *Corixa* (Benwitz 1956): ?; *Gelastocoris* (Parsons 1959): ?; *Lethocerus* (Parsons 1968): ?; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): ?; *Gerris* (Spangenberg et al. 2013b): ?; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): ?; *Triatoma* (Barth 1952a,b, 1953a,b): ?; *Dysdercus* (Khan 1972): ?; *Hackeriella* (Spangenberg et al. 2013a): ?; *Hemiodoecus* (Singh 1971): ?; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): ?; *Macrosiphum* (Singh 1971): ?; *Dactylosphaera* (Rilling 1960): ?; *Trialeurodes* (Weber 1935): ?; *Aleurolobus* (Singh 1971): ?; *Aleyrodes* (ps): ?; *Psylla* (Weber 1929): ?; *Diaphorina* (Singh 1971): ?; *Cacopsylla* (ps): ?; *Pseudococcus* (ps): ?; *Perissopneumon* (Singh 1971): ?; *Tibicina* (Snodgrass 1927; Kramer 1950): ?; *Idiocerus* (Arora & Singh 1962): ?; *Philaenus* (ps): ?; *Lepyronia* (Kramer 1950): ?; *Platypleura* (Singh 1971): ?; *Oxyrhachis* (Singh 1971): ?; *Scolops* (Kramer 1950): ?; *Melicharia* (Singh 1971): ?; *Dictyophara* (ps): ?; *Aeolothrips fasciatus* (Mickoleit 1963): 27 (The homology in Thysanoptera implies a shift of the insertion from the dorsaobasal edge of the paragloassa to the lateral edge of the prementum.) (Fig. 6B); *Aeolothrips intermedius* (Moritz 1982b): M.28 (Fig. 6B); *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): M.31; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): 27; *Oniscigaster* (Staniczek 2001): M56; *Zorotypus* (Beutel & Weide 2005): M.31; *Perla* (Chisholm 1962): -

0la12, M. praementoglossalis
Systelloderes (Spangenberg et al. 2013b): ?; *Cryptostemma* (Spangenberg et al. 2013b): ?; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): ?; *Corixa* (Benwitz 1956): ?; *Gelastocoris* (Parsons 1959): ?; *Lethocerus* (Parsons 1968): ?; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): ?; *Gerris* (Spangenberg et al. 2013b): ?; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): ?; *Triatoma* (Barth 1952a,b, 1953a,b): ?; *Dysdercus* (Khan 1972): ?; *Hackeriella* (Spangenberg et al. 2013a): ?; *Hemiodoecus* (Singh 1971): ?; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): ?; *Macrosiphum* (Singh 1971): ?; *Dactylosphaera* (Rilling 1960): ?; *Trialeurodes* (Weber 1935): ?; *Aleurolobus* (Singh 1971): ?; *Aleyrodes* (ps): ?; *Psylla* (Weber 1929): ?; *Diaphorina* (Singh 1971): ?; *Cacopsylla* (ps): ?; *Pseudococcus* (ps): ?; *Perissopneumon* (Singh 1971): ?; *Tibicina* (Snodgrass 1927; Kramer 1950): ?; *Idiocerus* (Arora & Singh 1962): ?; *Philaenus* (ps): ?; *Lepyronia* (Kramer 1950): ?; *Platypleura* (Singh 1971): ?; *Oxyrhachis* (Singh 1971): ?; *Scolops* (Kramer 1950): ?; *Melicharia* (Singh 1971): ?; *Dictyophara* (ps): ?; *Aeolothrips fasciatus* (Mickoleit 1963): 20 (Fig. 6B); *Aeolothrips intermedius* (Moritz 1982b): M.27 (Fig. 6B); *Thrips* (Risler 1957): 11; *Haplothrips* (Mickoleit 1963): 20; *Phlaeothrips* (Mickoleit 1963): 20; *Psocus* (Cope 1940): /;

Psococerastis (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): i (Fig. 6A); *Caecilius* (ps): +; *Cerobasis* (ps): +; *Troctes* (Noland 1924): /; *Liposcelis* (ps): + (Figs. 18F,G); *Gliricola* (Risler & Geising 1965): 16; *Myrsidea* (Buckup 1959): 22; *Pseudomenopon* (Haub 1967): 22; *Piagetiella* (ps): + (Fig. 20E); *Trochiloecetes* (Haub 1983): 2.4.2.2.; *Trimenopon* (Stöwe 1943): i; *Bovicola* (Risler 1951): 17; *Ornithobius* (Haub 1971): 4.4.1.5.; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): 17 (Fig. 6D); *Hybophthirus* (Tröster 1990a): M29; *Pediculus* (ps): + (Fig. 25H); *Phthirus* (Hirsch 1986): M11; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): M.32; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): 28; *Oniscigaster* (Staniczek 2001): M55; *Zorotypus* (Beutel & Weide 2005): M.32; *Perla* (Chisholm 1962): -

0la13, M. praementopalpalis internus

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): 22 (Fig. 6B); *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): M33; *Schizodactylus* (Khattar 1964): 32; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): M.33; *Perla* (Chisholm 1962): -

0la14, M. praementopalpalis externus

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): 21 (Fig. 6B); *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): 12; *Haplothrips* (Mickoleit 1963): 21; *Phlaeothrips* (Mickoleit 1963): 21; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): l (Fig. 6A); *Caecilius* (ps): +; *Cerobasis* (ps): +; *Troctes* (Noland 1924): /; *Liposcelis* (ps): +; *Gliricola* (Risler & Geising 1965): 15; *Myrsidea* (Buckup 1959): 21; *Pseudomenopon* (Haub 1967): 21; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon*

(Stöwe 1943): l; *Bovicola* (Risler 1951): 16; *Ornithobius* (Haub 1971): 4.4.1.4.; *Columbicola* (ps): + (Fig. 22E); *Haematopinus* (Ramcke 1965): 18 (Fig. 6D); *Hybophthirus* (Tröster 1990a): M30; *Pediculus* (ps): + (Fig. 25G); *Phthirus* (Hirsch 1986): M12; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): M.34; *Osmylus* (Beutel et al. 2010): M34; *Schizodactylus* (Khattar 1964): 31; *Oniscigaster* (Staniczek 2001): M50; *Zorotypus* (Beutel & Weide 2005): M.34; *Perla* (Chisholm 1962): -

0la15, M. praementomembranus
absent in all taxa examined and not mentioned in other studies

0la16, M. palpopalpalis labii primus
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): g (Fig. 6A); *Caecilius* (ps): +; *Cerobasis* (ps): + (Fig. 16G); *Troctes* (Noland 1924): /; *Liposcelis* (ps): +; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): M35; *Schizodactylus* (Khattar 1964): 33; *Oniscigaster* (Staniczek 2001): M51; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

0la17, M. palpopalpalis labii secundus
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke

1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): M.36; *Osmylus* (Beutel et al. 2010): M36; *Schizodactylus* (Khattar 1964): 34; *Oniscigaster* (Staniczek 2001): M54; *Zorotypus* (Beutel & Weide 2005): M.36; *Perla* (Chisholm 1962): -

0lax1, labial abductor of Hemiptera
Systelloderes (Spangenberg et al. 2013b): M19; *Cryptostemma* (Spangenberg et al. 2013b): M19; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): KM3; *Corixa* (Benwitz 1956): depr lb1; *Gelastocoris* (Parsons 1959): KM3; *Lethocerus* (Parsons 1968): H3B; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): KM3; *Gerris* (Spangenberg et al. 2013b): M19; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): 3; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): M19; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): m. abd2 (Fig. 6C); *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): m. add. lab1; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): +; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): + (Fig. 11C); *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): ?; *Caecilius* (ps): ?; *Cerobasis* (ps): ?; *Troctes* (Noland 1924): /; *Liposcelis* (ps): ?; *Gliricola* (Risler & Geising 1965): ?; *Myrsidea* (Buckup 1959): ?; *Pseudomenopon* (Haub 1967): ?; *Piagetiella* (ps): ?; *Trochiloecetes* (Haub 1983): ?; *Trimenopon* (Stöwe 1943): ?; *Bovicola* (Risler 1951): ?; *Ornithobius* (Haub 1971): ?; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): ?; *Hybophthirus* (Tröster 1990a): ?; *Pediculus* (ps): ?; *Phthirus* (Hirsch 1986): ?; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): ?; *Osmylus* (Beutel et al. 2010): ?; *Schizodactylus* (Khattar 1964): ?; *Oniscigaster* (Staniczek 2001): ?; *Zorotypus* (Beutel & Weide 2005): ?; *Perla* (Chisholm 1962): ?

0lax2, labial adductor of Hemiptera
Systelloderes (Spangenberg et al. 2013b): M17a; *Cryptostemma* (Spangenberg et al. 2013b): M17a; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): KM1; *Corixa* (Benwitz 1956): add lb1; *Gelastocoris* (Parsons 1959): KM1; *Lethocerus* (Parsons 1968): H1; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): KM1; *Gerris* (Spangenberg et al. 2013b): M17a; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): 1; *Triatoma* (Barth 1952a,b, 1953a,b): ? (Mu16); *Dysdercus* (Khan 1972): ? (ABL); *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): 15; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): m. add1 (Fig. 6C); *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): m. protr. Cru.; *Aleurolobus* (Singh 1971): 15; *Aleyrodes* (ps): +; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): +; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): plb; *Idiocerus* (Arora & Singh 1962): 15; *Philaenus* (ps): +; *Lepyronia* (Kramer 1950): plb; *Platypleura* (Singh 1971): 15; *Oxyrhachis* (Singh 1971): 15; *Scolops* (Kramer 1950): plb; *Melicharia* (Singh 1971): 15; *Dictyophara* (ps): + (Fig. 14A); *Aeolothrips fasciatus* (Mickoleit 1963): ?; *Aeolothrips intermedius* (Moritz 1982b): ?; *Thrips* (Risler 1957): ?; *Haplothrips* (Mickoleit 1963): ?; *Phlaeothrips* (Mickoleit 1963): ?; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): ?; *Caecilius* (ps): ?; *Cerobasis* (ps): ?; *Troctes* (Noland 1924): /; *Liposcelis* (ps): ?; *Gliricola* (Risler & Geising 1965): ?; *Myrsidea* (Buckup 1959): ?; *Pseudomenopon* (Haub 1967): ?; *Piagetiella* (ps): ?; *Trochiloecetes* (Haub 1983): ?; *Trimenopon* (Stöwe 1943): ?; *Bovicola* (Risler 1951): ?; *Ornithobius* (Haub 1971): ?; *Columbicola* (ps): ?; *Haematopinus* (Ramcke 1965): ?; *Hybophthirus* (Tröster 1990a): ?; *Pediculus* (ps): ?; *Phthirus* (Hirsch 1986): ?; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): ?; *Osmylus* (Beutel et al.

2010): ?; *Schizodactylus* (Khattar 1964): ?; *Oniscigaster* (Staniczek 2001): ?; *Zorotypus* (Beutel & Weide 2005): ?; *Perla* (Chisholm 1962): ?

0lax3, labial adductor of Hemiptera
Systelloderes (Spangenberg et al. 2013b): M18; *Cryptostemma* (Spangenberg et al. 2013b): M18; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): KM2a; *Corixa* (Benwitz 1956): add lb2; *Gelastocoris* (Parsons 1959): KM2; *Lethocerus* (Parsons 1968): H2A; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): KM2a; *Gerris* (Spangenberg et al. 2013b): M18; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): 1.5; *Triatoma* (Barth 1952a,b, 1953a,b): Mu4; *Dysdercus* (Khan 1972): ? (ABL); *Hackeriella* (Spangenberg et al. 2013a): M18; *Hemiodoecus* (Singh 1971): 17; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): m. add2 (Fig. 6C); *Macrosiphum* (Singh 1971): 17; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): m. add2.; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): 17; *Cacopsylla* (ps): -; *Pseudococcus* (ps): +; *Perissopneumon* (Singh 1971): 17; *Tibicina* (Snodgrass 1927; Kramer 1950): rlb; *Idiocerus* (Arora & Singh 1962): 16; *Philaenus* (ps): +; *Lepyronia* (Kramer 1950): rlb; *Platypleura* (Singh 1971): 17; *Oxyrhachis* (Singh 1971): 17; *Scolops* (Kramer 1950): rlb; *Melicharia* (Singh 1971): 17; *Dictyophara* (ps): + (Fig. 14A); *Aeolothrips fasciatus* (Mickoleit 1963): ?; *Aeolothrips intermedius* (Moritz 1982b): ?; *Thrips* (Risler 1957): ?; *Haplothrips* (Mickoleit 1963): ?; *Phlaeothrips* (Mickoleit 1963): ?; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): ?; *Caecilius* (ps): ?; *Cerobasis* (ps): ?; *Troctes* (Noland 1924): /; *Liposcelis* (ps): ?; *Gliricola* (Risler & Geising 1965): ?; *Myrsidea* (Buckup 1959): ?; *Pseudomenopon* (Haub 1967): ?; *Piagetiella* (ps): ?; *Trochiloecetes* (Haub 1983): ?; *Trimenopon* (Stöwe 1943): ?; *Bovicola* (Risler 1951): ?; *Ornithobius* (Haub 1971): ?; *Columbicola* (ps): ?; *Haematopinus* (Ramcke 1965): ?; *Hybophthirus* (Tröster 1990a): ?; *Pediculus* (ps): ?; *Phthirus* (Hirsch 1986): ?; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): ?; *Osmylus* (Beutel et al. 2010): ?; *Schizodactylus* (Khattar 1964): ?; *Oniscigaster* (Staniczek 2001): ?; *Zorotypus* (Beutel & Weide 2005): ?; *Perla* (Chisholm 1962): ?

0lax4, labial adductor of Hemiptera
Systelloderes (Spangenberg et al. 2013b): M20; *Cryptostemma* (Spangenberg et al. 2013b): M20; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): KM4; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): KM4; *Lethocerus* (Parsons 1968): H4; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): KM4; *Gerris* (Spangenberg et al. 2013b): M20; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): 4; *Triatoma* (Barth 1952a,b, 1953a,b): MUD proximal; *Dysdercus* (Khan 1972): ADL2; *Hackeriella* (Spangenberg et al. 2013a): M20; *Hemiodoecus* (Singh 1971): 23 (+24); *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): m. add3 (Fig. 6C); *Macrosiphum* (Singh 1971): 23; *Dactylosphaera* (Rilling 1960): 29; *Trialeurodes* (Weber 1935): m. trans1.; *Aleurolobus* (Singh 1971): 23; *Aleyrodes* (ps): +; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): +; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): mlb1; *Idiocerus* (Arora & Singh 1962): 17; *Philaenus* (ps): + (Fig. 12D); *Lepyronia* (Kramer 1950): mlb1; *Platypleura* (Singh 1971): 23; *Oxyrhachis* (Singh 1971): 23; *Scolops* (Kramer 1950): mlb1; *Melicharia* (Singh 1971): 23; *Dictyophara* (ps): + (Fig. 14B); *Aeolothrips fasciatus* (Mickoleit 1963): ?; *Aeolothrips intermedius* (Moritz 1982b): ?; *Thrips* (Risler 1957): ?; *Haplothrips* (Mickoleit 1963): ?; *Phlaeothrips* (Mickoleit 1963): ?; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): ?; *Caecilius* (ps): ?; *Cerobasis* (ps): ?; *Troctes* (Noland 1924): /; *Liposcelis* (ps): ?; *Gliricola* (Risler & Geising 1965): ?; *Myrsidea* (Buckup 1959): ?; *Pseudomenopon* (Haub 1967): ?; *Piagetiella* (ps): ?; *Trochiloecetes* (Haub 1983): ?; *Trimenopon* (Stöwe 1943): ?; *Bovicola* (Risler 1951): ?; *Ornithobius* (Haub 1971): ?; *Columbicola* (ps): ?; *Haematopinus* (Ramcke 1965): ?; *Hybophthirus* (Tröster 1990a): ?; *Pediculus* (ps): ?; *Phthirus* (Hirsch 1986): ?; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): ?; *Osmylus* (Beutel et al. 2010): ?; *Schizodactylus* (Khattar 1964): ?; *Oniscigaster* (Staniczek 2001): ?; *Zorotypus* (Beutel & Weide 2005): ?; *Perla* (Chisholm 1962): ?

0lax5, labial adductor of Hemiptera
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): m. add4 (Fig. 6C); *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): 31; *Trialeurodes* (Weber 1935): -.; *Aleurolobus* (Singh 1971): 25; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): 25; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): ?; *Aeolothrips intermedius* (Moritz 1982b): ?; *Thrips* (Risler 1957): ?; *Haplothrips* (Mickoleit 1963): ?; *Phlaeothrips* (Mickoleit 1963): ?; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): ?; *Caecilius* (ps): ?; *Cerobasis* (ps): ?; *Troctes* (Noland 1924): /; *Liposcelis* (ps): ?; *Gliricola* (Risler & Geising 1965): ?; *Myrsidea* (Buckup 1959): ?; *Pseudomenopon* (Haub 1967): ?; *Piagetiella* (ps): ?; *Trochiloecetes* (Haub 1983): ?; *Trimenopon* (Stöwe 1943): ?; *Bovicola* (Risler 1951): ?; *Ornithobius* (Haub 1971): ?; *Columbicola* (ps): ?; *Haematopinus* (Ramcke 1965): ?; *Hybophthirus* (Tröster 1990a): ?; *Pediculus* (ps): ?; *Phthirus* (Hirsch 1986): ?; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): ?; *Osmylus* (Beutel et al. 2010): ?; *Schizodactylus* (Khattar 1964): ?; *Oniscigaster* (Staniczek 2001): ?; *Zorotypus* (Beutel & Weide 2005): ?; *Perla* (Chisholm 1962): ?

0lax6, labial adductor of Hemiptera
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): m. add5 (Fig. 6C); *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): 30; *Trialeurodes* (Weber 1935): -.; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): ?; *Aeolothrips intermedius* (Moritz 1982b): ?; *Thrips* (Risler 1957): ?; *Haplothrips* (Mickoleit 1963): ?; *Phlaeothrips* (Mickoleit 1963): ?; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): ?; *Caecilius* (ps): ?; *Cerobasis* (ps): ?; *Troctes* (Noland 1924): /; *Liposcelis* (ps): ?; *Gliricola* (Risler & Geising 1965): ?; *Myrsidea* (Buckup 1959): ?; *Pseudomenopon* (Haub 1967): ?; *Piagetiella* (ps): ?; *Trochiloecetes* (Haub 1983): ?; *Trimenopon* (Stöwe 1943): ?; *Bovicola* (Risler 1951): ?; *Ornithobius* (Haub 1971): ?; *Columbicola* (ps): ?; *Haematopinus* (Ramcke 1965): ?; *Hybophthirus* (Tröster 1990a): ?; *Pediculus* (ps): ?; *Phthirus* (Hirsch 1986): ?; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): ?; *Osmylus* (Beutel et al. 2010): ?; *Schizodactylus* (Khattar 1964): ?; *Oniscigaster* (Staniczek 2001): ?; *Zorotypus* (Beutel & Weide 2005): ?; *Perla* (Chisholm 1962): ?

0lax7, labial abductor of Hemiptera
Systelloderes (Spangenberg et al. 2013b): M22; *Cryptostemma* (Spangenberg et al. 2013b): M22; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): KM7a + KM7b; *Corixa* (Benwitz 1956): ? (deprlb2); *Gelastocoris* (Parsons 1959): KM7; *Lethocerus* (Parsons 1968):

H7; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): KM7; *Gerris* (Spangenberg et al. 2013b): M22; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): 7; *Triatoma* (Barth 1952a,b, 1953a,b): MUL; *Dysdercus* (Khan 1972): RLB; *Hackeriella* (Spangenberg et al. 2013a): M22; *Hemiodoecus* (Singh 1971): 30; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): m. abd3 (Fig. 6C); *Macrosiphum* (Singh 1971): 30; *Dactylosphaera* (Rilling 1960): 33 + 34; *Trialeurodes* (Weber 1935): m. abd.; *Aleurolobus* (Singh 1971): 30; *Aleyrodes* (ps): +; *Psylla* (Weber 1929): m. lab1; *Diaphorina* (Singh 1971): 30; *Cacopsylla* (ps): +; *Pseudococcus* (ps): + (Fig. 10F); *Perissopneumon* (Singh 1971): 30; *Tibicina* (Snodgrass 1927; Kramer 1950): mlb3; *Idiocerus* (Arora & Singh 1962): 21; *Philaenus* (ps): +; *Lepyronia* (Kramer 1950): mlb3 + mlb4; *Platypleura* (Singh 1971): 30; *Oxyrhachis* (Singh 1971): 30; *Scolops* (Kramer 1950): mlb3 + mlb4; *Melicharia* (Singh 1971): 30; *Dictyophara* (ps): + (Fig. 14C); *Aeolothrips fasciatus* (Mickoleit 1963): ?; *Aeolothrips intermedius* (Moritz 1982b): ?; *Thrips* (Risler 1957): ?; *Haplothrips* (Mickoleit 1963): ?; *Phlaeothrips* (Mickoleit 1963): ?; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): ?; *Caecilius* (ps): ?; *Cerobasis* (ps): ?; *Troctes* (Noland 1924): /; *Liposcelis* (ps): ?; *Gliricola* (Risler & Geising 1965): ?; *Myrsidea* (Buckup 1959): ?; *Pseudomenopon* (Haub 1967): ?; *Piagetiella* (ps): ?; *Trochiloecetes* (Haub 1983): ?; *Trimenopon* (Stöwe 1943): ?; *Bovicola* (Risler 1951): ?; *Ornithobius* (Haub 1971): ?; *Columbicola* (ps): ?; *Haematopinus* (Ramcke 1965): ?; *Hybophthirus* (Tröster 1990a): ?; *Pediculus* (ps): ?; *Phthirus* (Hirsch 1986): ?; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): ?; *Osmylus* (Beutel et al. 2010): ?; *Schizodactylus* (Khattar 1964): ?; *Oniscigaster* (Staniczek 2001): ?; *Zorotypus* (Beutel & Weide 2005): ?; *Perla* (Chisholm 1962): ?

0lax8, labial transversal muscle of Hemiptera

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): m. trans1 (Fig. 6C); *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): 32; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): ?; *Aeolothrips intermedius* (Moritz 1982b): ?; *Thrips* (Risler 1957): ?; *Haplothrips* (Mickoleit 1963): ?; *Phlaeothrips* (Mickoleit 1963): ?; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): ?; *Caecilius* (ps): ?; *Cerobasis* (ps): ?; *Troctes* (Noland 1924): /; *Liposcelis* (ps): ?; *Gliricola* (Risler & Geising 1965): ?; *Myrsidea* (Buckup 1959): ?; *Pseudomenopon* (Haub 1967): ?; *Piagetiella* (ps): ?; *Trochiloecetes* (Haub 1983): ?; *Trimenopon* (Stöwe 1943): ?; *Bovicola* (Risler 1951): ?; *Ornithobius* (Haub 1971): ?; *Columbicola* (ps): ?; *Haematopinus* (Ramcke 1965): ?; *Hybophthirus* (Tröster 1990a): ?; *Pediculus* (ps): ?; *Phthirus* (Hirsch 1986): ?; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): ?; *Osmylus* (Beutel et al. 2010): ?; *Schizodactylus* (Khattar 1964): ?; *Oniscigaster* (Staniczek 2001): ?; *Zorotypus* (Beutel & Weide 2005): ?; *Perla* (Chisholm 1962): ?

0lax9, labial transversal muscle of Hemiptera

Systelloderes (Spangenberg et al. 2013b): M20a; *Cryptostemma* (Spangenberg et al. 2013b): M20a; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): KM5; *Corixa* (Benwitz 1956): trans Ib; *Gelastocoris* (Parsons 1959): KM5; *Lethocerus* (Parsons 1968): H5; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): KM5; *Gerris* (Spangenberg et al. 2013b): M20a; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): 5; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): ADL3; *Hackeriella*

(Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): m. trans2-4 (Fig. 6C); *Macrosiphum* (Singh 1971): 24; *Dactylosphaera* (Rilling 1960): 35; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): 24; *Aleyrodes* (ps): +; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): 24; *Cacopsylla* (ps): -; *Pseudococcus* (ps): + (Fig. 11C); *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): mlb2; *Idiocerus* (Arora & Singh 1962): 18; *Philaenus* (ps): +; *Lepyronia* (Kramer 1950): mlb2; *Platypleura* (Singh 1971): 24; *Oxyrhachis* (Singh 1971): 24; *Scolops* (Kramer 1950): mlb2; *Melicharia* (Singh 1971): 24; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): ?; *Aeolothrips intermedius* (Moritz 1982b): ?; *Thrips* (Risler 1957): ?; *Haplothrips* (Mickoleit 1963): ?; *Phlaeothrips* (Mickoleit 1963): ?; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): ?; *Caecilius* (ps): ?; *Cerobasis* (ps): ?; *Troctes* (Noland 1924): /; *Liposcelis* (ps): ?; *Gliricola* (Risler & Geising 1965): ?; *Myrsidea* (Buckup 1959): ?; *Pseudomenopon* (Haub 1967): ?; *Piagetiella* (ps): ?; *Trochiloecetes* (Haub 1983): ?; *Trimenopon* (Stöwe 1943): ?; *Bovicola* (Risler 1951): ?; *Ornithobius* (Haub 1971): ?; *Columbicola* (ps): ?; *Haematopinus* (Ramcke 1965): ?; *Hybophthirus* (Tröster 1990a): ?; *Pediculus* (ps): ?; *Phthirus* (Hirsch 1986): ?; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): ?; *Osmylus* (Beutel et al. 2010): ?; *Schizodactylus* (Khattar 1964): ?; *Oniscigaster* (Staniczek 2001): ?; *Zorotypus* (Beutel & Weide 2005): ?; *Perla* (Chisholm 1962): ?

0lax10, labial transversal muscle of Hemiptera

Systelloderes (Spangenberg et al. 2013b): M21; *Cryptostemma* (Spangenberg et al. 2013b): M21; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): KM6; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): KM6; *Lethocerus* (Parsons 1968): H6; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): KM6; *Gerris* (Spangenberg et al. 2013b): M21; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): 6; *Triatoma* (Barth 1952a,b, 1953a,b): MUD distal; *Dysdercus* (Khan 1972): TLB1; *Hackeriella* (Spangenberg et al. 2013a): M21; *Hemiodoecus* (Singh 1971): 26; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): m. trans5 (Fig. 6C); *Macrosiphum* (Singh 1971): 26; *Dactylosphaera* (Rilling 1960): 35; *Trialeurodes* (Weber 1935): m. trans2-3; *Aleurolobus* (Singh 1971): 26; *Aleyrodes* (ps): +; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): +; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): 19 + 20; *Philaenus* (ps): + (Fig. 12E); *Lepyronia* (Kramer 1950): mlb5; *Platypleura* (Singh 1971): 26; *Oxyrhachis* (Singh 1971): 26; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): 26; *Dictyophara* (ps): + (Fig. 14C); *Aeolothrips fasciatus* (Mickoleit 1963): ?; *Aeolothrips intermedius* (Moritz 1982b): ?; *Thrips* (Risler 1957): ?; *Haplothrips* (Mickoleit 1963): ?; *Phlaeothrips* (Mickoleit 1963): ?; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): ?; *Caecilius* (ps): ?; *Cerobasis* (ps): ?; *Troctes* (Noland 1924): /; *Liposcelis* (ps): ?; *Gliricola* (Risler & Geising 1965): ?; *Myrsidea* (Buckup 1959): ?; *Pseudomenopon* (Haub 1967): ?; *Piagetiella* (ps): ?; *Trochiloecetes* (Haub 1983): ?; *Trimenopon* (Stöwe 1943): ?; *Bovicola* (Risler 1951): ?; *Ornithobius* (Haub 1971): ?; *Columbicola* (ps): ?; *Haematopinus* (Ramcke 1965): ?; *Hybophthirus* (Tröster 1990a): ?; *Pediculus* (ps): ?; *Phthirus* (Hirsch 1986): ?; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): ?; *Osmylus* (Beutel et al. 2010): ?; *Schizodactylus* (Khattar 1964): ?; *Oniscigaster* (Staniczek 2001): ?; *Zorotypus* (Beutel & Weide 2005): ?; *Perla* (Chisholm 1962): ?

0lax11, basal labial muscle of Hemiptera

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): Ovlm3; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960):

27; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): + (Fig. 10G); *Perissopneumon* (Singh 1971): 21; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): 21; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

0lax12, muscle of labial crumena of Hemiptera

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): 22; *Cacopsylla* (ps): +; *Pseudococcus* (ps): + (Fig. 10G); *Perissopneumon* (Singh 1971): 22; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

0lax13, basal labial muscle of Hemiptera

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): + (Figs. 10G,H); *Perissopneumon* (Singh 1971): 16; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -;

Scolops (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

0lax14, labial abductor of Hemiptera

Systelloderes (Spangenberg et al. 2013b): M17; *Cryptostemma* (Spangenberg et al. 2013b): M17; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): KM2b; *Corixa* (Benwitz 1956): MuFa; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): H2B; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): KM2b; *Gerris* (Spangenberg et al. 2013b): M17; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): 2; *Triatoma* (Barth 1952a,b, 1953a,b): Mu5; *Dysdercus* (Khan 1972): ADL1; *Hackeriella* (Spangenberg et al. 2013a): M17 (Fig. 7E); *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): m. abd1 (Fig. 6C); *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): m. retr. lab2; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): +; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): +; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): 14; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): +; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): ?; *Caecilius* (ps): ?; *Cerobasis* (ps): ?; *Troctes* (Noland 1924): /; *Liposcelis* (ps): ?; *Gliricola* (Risler & Geising 1965): ?; *Myrsidea* (Buckup 1959): ?; *Pseudomenopon* (Haub 1967): ?; *Piagetiella* (ps): ?; *Trochiloecetes* (Haub 1983): ?; *Trimenopon* (Stöwe 1943): ?; *Bovicola* (Risler 1951): ?; *Ornithobius* (Haub 1971): ?; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): ?; *Hybophthirus* (Tröster 1990a): ?; *Pediculus* (ps): ?; *Phthirus* (Hirsch 1986): ?; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): ?; *Osmylus* (Beutel et al. 2010): ?; *Schizodactylus* (Khattar 1964): ?; *Oniscigaster* (Staniczek 2001): ?; *Zorotypus* (Beutel & Weide 2005): ?; *Perla* (Chisholm 1962): ?

0lax15, labial muscle of Hemiptera

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): H3A; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): ?; *Aeolothrips intermedius* (Moritz 1982b): ?; *Thrips* (Risler 1957): ?; *Haplothrips* (Mickoleit 1963): ?; *Phlaeothrips* (Mickoleit 1963): ?; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima

1993): /; *Stenopsocus* (Badonnel 1934): ?; *Caecilius* (ps): ?; *Cerobasis* (ps): ?; *Troctes* (Noland 1924): /; *Liposcelis* (ps): ?; *Gliricola* (Risler & Geising 1965): ?; *Myrsidea* (Buckup 1959): ?; *Pseudomenopon* (Haub 1967): ?; *Piagetiella* (ps): ?; *Trochiloecetes* (Haub 1983): ?; *Trimenopon* (Stöwe 1943): ?; *Bovicola* (Risler 1951): ?; *Ornithobius* (Haub 1971): ?; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): ?; *Hybophthirus* (Tröster 1990a): ?; *Pediculus* (ps): ?; *Phthirus* (Hirsch 1986): ?; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): ?; *Osmylus* (Beutel et al. 2010): ?; *Schizodactylus* (Khattar 1964): ?; *Oniscigaster* (Staniczek 2001): ?; *Zorotypus* (Beutel & Weide 2005): ?; *Perla* (Chisholm 1962): ?

0lax16, transversal labial muscle of Hemiptera

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): 36; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): 29; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): ?; *Aeolothrips intermedius* (Moritz 1982b): ?; *Thrips* (Risler 1957): ?; *Haplothrips* (Mickoleit 1963): ?; *Phlaeothrips* (Mickoleit 1963): ?; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): ?; *Caecilius* (ps): ?; *Cerobasis* (ps): ?; *Troctes* (Noland 1924): /; *Liposcelis* (ps): ?; *Gliricola* (Risler & Geising 1965): ?; *Myrsidea* (Buckup 1959): ?; *Pseudomenopon* (Haub 1967): ?; *Piagetiella* (ps): ?; *Trochiloecetes* (Haub 1983): ?; *Trimenopon* (Stöwe 1943): ?; *Bovicola* (Risler 1951): ?; *Ornithobius* (Haub 1971): ?; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): ?; *Hybophthirus* (Tröster 1990a): ?; *Pediculus* (ps): ?; *Phthirus* (Hirsch 1986): ?; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): ?; *Osmylus* (Beutel et al. 2010): ?; *Schizodactylus* (Khattar 1964): ?; *Oniscigaster* (Staniczek 2001): ?; *Zorotypus* (Beutel & Weide 2005): ?; *Perla* (Chisholm 1962): ?

0lax17, basal labial muscle of Hemiptera

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): Oism; *Macrosiphum* (Singh 1971): 18; *Dactylosphaera* (Rilling 1960): 28 (+26?); *Trialeurodes* (Weber 1935): Oism2+3; *Aleurolobus* (Singh 1971): 18; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): Oism1+2; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): +; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -;

Haematopinus (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

0lax18, additional set of transversal musles at distal end of L3 of Hemiptera
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): 28; *Cacopsylla* (ps): -; *Pseudococcus* (ps): +; *Perissopneumon* (Singh 1971): 28; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): 28; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): 28; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): ?; *Aeolothrips intermedius* (Moritz 1982b): ?; *Thrips* (Risler 1957): ?; *Haplothrips* (Mickoleit 1963): ?; *Phlaeothrips* (Mickoleit 1963): ?; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): ?; *Caecilius* (ps): ?; *Cerobasis* (ps): ?; *Troctes* (Noland 1924): /; *Liposcelis* (ps): ?; *Gliricola* (Risler & Geising 1965): ?; *Myrsidea* (Buckup 1959): ?; *Pseudomenopon* (Haub 1967): ?; *Piagetiella* (ps): ?; *Trochiloecetes* (Haub 1983): ?; *Trimenopon* (Stöwe 1943): ?; *Bovicola* (Risler 1951): ?; *Ornithobius* (Haub 1971): ?; *Columbicola* (ps): ?; *Haematopinus* (Ramcke 1965): ?; *Hybophthirus* (Tröster 1990a): ?; *Pediculus* (ps): ?; *Phthirus* (Hirsch 1986): ?; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): ?; *Osmylus* (Beutel et al. 2010): ?; *Schizodactylus* (Khattar 1964): ?; *Oniscigaster* (Staniczek 2001): ?; *Zorotypus* (Beutel & Weide 2005): ?; *Perla* (Chisholm 1962): ?

0lax19, basal labial muscle of Hemiptera
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): 19; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): m. retr. lab1; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): 19; *Cacopsylla* (ps): +; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): 19; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

0lax20, labial muscle of Hemiptera
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): 20; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

0lax21, "M. palpopalpalis labii primus lateralis"
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): M.35; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): M52; *Zorotypus* (Beutel & Weide 2005): M.35; *Perla* (Chisholm 1962): -

0lax22, "M. palpopalpalis labii primus anterior"
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al.

1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): M53; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

0lax23, labial muscle of Hemiptera

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): m. add. lab3; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): 27; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): 27; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): ?; *Aeolothrips intermedius* (Moritz 1982b): ?; *Thrips* (Risler 1957): ?; *Haplothrips* (Mickoleit 1963): ?; *Phlaeothrips* (Mickoleit 1963): ?; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): ?; *Caecilius* (ps): ?; *Cerobasis* (ps): ?; *Troctes* (Noland 1924): /; *Liposcelis* (ps): ?; *Gliricola* (Risler & Geising 1965): ?; *Myrsidea* (Buckup 1959): ?; *Pseudomenopon* (Haub 1967): ?; *Piagetiella* (ps): ?; *Trochiloecetes* (Haub 1983): ?; *Trimenopon* (Stöwe 1943): ?; *Bovicola* (Risler 1951): ?; *Ornithobius* (Haub 1971): ?; *Columbicola* (ps): ?; *Haematopinus* (Ramcke 1965): ?; *Hybophthirus* (Tröster 1990a): ?; *Pediculus* (ps): ?; *Phthirus* (Hirsch 1986): ?; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): ?; *Osmylus* (Beutel et al. 2010): ?; *Schizodactylus* (Khattar 1964): ?; *Oniscigaster* (Staniczek 2001): ?; *Zorotypus* (Beutel & Weide 2005): ?; *Perla* (Chisholm 1962): ?

Muscles of the hypopharynx

0hy1, M. frontooralis

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -;

Hemiodoecus (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): C1 + C2 (Fig. 7A). The homology of the “muscles fronto-pharyngiens latéraux” of *Stenopsocus* is unclear according to Badonnel (1934). This muscle was described for the first time in chapter II on the stomadeum and its musculature (p. 26 in Badonnel 1934). “Muscles fronto-pharyngiens latéraux” originate always on the frons between the ocelli and epistomal ridge (fig. 13 of Badonnel 1934). It inserts on the dorsal buccal wall on the oral arm of the hypopharynx (“et d’autre part sur l’angle buccal, à l’extrémité des bras oraux de l’hypopharynx”). This is somewhat ambiguous as there is either a muscle inserting on the bucca (0bu2, 0bu3 of Wipfler et al. 2011) or on the oral arms of the hypopharynx (0hy1 of Wipfler et al. 2011) in generalized insects. In fig. 11 of Badonnel (1934) the “muscles fronto-pharyngiens latéraux” apparently insert directly on the oral hypopharyngeal arm, but they are also shown in his fig. 13 which only covers labral and pharyngeal muscles. Badonnel (1934) described the muscle again in the chapter dealing with the hypopharynx and suggested that it is homologous to the fronto-hypopharyngeal muscle in Orthoptera. This interpretation is followed here and was also adopted by Matsuda (1965), who also mentioned two muscles (or portions of a single muscle?) inserting on the oral hypopharyngeal arm in *Stenopsocus*; *Caecilius* (ps): +; *Cerobasis* (ps): + (Figs. 7B, 16B); *Troctes* (Noland 1924): /; *Liposcelis* (ps): + (Fig. 18E); *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): 27a-d; *Pseudomenopon* (Haub 1967): 27; *Piagetiella* (ps): + (Fig. 20E); *Trochiloecetes* (Haub 1983): 3.3.2.1.; *Trimenopon* (Stöwe 1943): Mh + C; *Bovicola* (Risler 1951): 25a-c; *Ornithobius* (Haub 1971): 6.1.3.; *Columbicola* (ps): + (Figs. 7C, 22F); *Haematopinus* (Ramcke 1965): 6; *Hybophthirus* (Tröster 1990a): M11 (Fig. 7F); *Pediculus* (ps): + (Fig. 25E); *Phthirus* (Hirsch 1986): M21; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): M.41 + M.43b; *Osmylus* (Beutel et al. 2010): M41a; *Schizodactylus* (Khattar 1964): 43; *Oniscigaster* (Staniczek 2001): M18; *Zorotypus* (Beutel & Weide 2005): M.41; *Perla* (Chisholm 1962): E. M. A.

0hy2, M. tentorioralis

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): + (Fig. 7B); *Troctes* (Noland 1924): /; *Liposcelis* (ps): + (Fig. 18H); *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): Tentorio-Oralligament; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): Lig2 (see Tröster (1990a) p. 20); *Hybophthirus*

(Tröster 1990a): Lig2 (Fig. 7F); *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): M41b; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): M19; *Zorotypus* (Beutel & Weide 2005): M.47; *Perla* (Chisholm 1962): -

0hy3, M. craniohypopharyngealis
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): M45; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): HYP. RET.

0hy4, M. postoccipitalohypopharyngealis
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): 26 (Fig. 7D); *Aeolothrips intermedius* (Moritz 1982b): M.13 (Fig. 7D); *Thrips* (Risler 1957): 16; *Haplothrips* (Mickoleit 1963): 26; *Phlaeothrips* (Mickoleit 1963): 26; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): r (Fig. 7A); *Caecilius* (ps): +; *Cerobasis* (ps): + (Figs. 7B, 16F,G); *Troctes* (Noland 1924): /; *Liposcelis* (ps): + (Fig. 18I); *Gliricola* (Risler & Geising 1965): 11; *Myrsidea* (Buckup 1959): 25; *Pseudomenopon* (Haub 1967): 25; *Piagetiella* (ps): + (Figs. 20F,G,H); *Trochiloecetes* (Haub 1983): 3.3.2.4.; *Trimenopon* (Stöwe 1943): Mr; *Bovicola* (Risler 1951): 20; *Ornithobius* (Haub 1971): 6.1.1.; *Columbicola* (ps): + (Figs. 7C, 22G); *Haematopinus* (Ramcke 1965): 22; *Hybophthirus* (Tröster 1990a): M28 (Fig. 7F); *Pediculus* (ps): + (Fig. 25I); *Phthirus* (Hirsch 1986): M9; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): 35; *Oniscigaster* (Staniczek 2001): -;

Zorotypus (Beutel & Weide 2005): ? (mxz, homologization impeded by the insertion on the salivarium or salivary sclerites, instead of a direct insertion on the posterior hypopharynx); *Perla* (Chisholm 1962): -

0hy5, M. tentoriosuspensorialis
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): +; *Cerobasis* (ps): + (Figs. 7B, 16C,D); *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): 26; *Pseudomenopon* (Haub 1967): 26; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): 3.3.2.3.; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): 22; *Ornithobius* (Haub 1971): 6.1.2.; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): M.42; *Osmylus* (Beutel et al. 2010): M42; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): M.42; *Perla* (Chisholm 1962): HYP. DEP.

0hy6, M. postmentoloralis
absent in all taxa examined and not mentioned in other studies

0hy7, M. praementosalivaris anterior
Systelloderes (Spangenberg et al. 2013b): ?; *Cryptostemma* (Spangenberg et al. 2013b): ?; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): ?; *Corixa* (Benwitz 1956): ?; *Gelastocoris* (Parsons 1959): ?; *Lethocerus* (Parsons 1968): ?; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): ?; *Gerris* (Spangenberg et al. 2013b): ?; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): ?; *Triatoma* (Barth 1952a,b, 1953a,b): ?; *Dysdercus* (Khan 1972): ?; *Hackeriella* (Spangenberg et al. 2013a): ?; *Hemiodoecus* (Singh 1971): ?; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): ?; *Macrosiphum* (Singh 1971): ?; *Dactylosphaera* (Rilling 1960): ?; *Trialeurodes* (Weber 1935): ?; *Aleurolobus* (Singh 1971): ?; *Aleyrodes* (ps): ?; *Psylla* (Weber 1929): ?; *Diaphorina* (Singh 1971): ?; *Cacopsylla* (ps): ?; *Pseudococcus* (ps): ?; *Perissopneumon* (Singh 1971): ?; *Tibicina* (Snodgrass 1927; Kramer 1950): ?; *Idiocerus* (Arora & Singh 1962): ?; *Philaenus* (ps): ?; *Lepyronia* (Kramer 1950): ?; *Platypleura* (Singh 1971): ?; *Oxyrhachis* (Singh 1971): ?; *Scolops* (Kramer 1950): ?; *Melicharia* (Singh 1971): ?; *Dictyophara* (ps): ?; *Aeolothrips fasciatus* (Mickoleit 1963): 24 (Fig. 6B); *Aeolothrips intermedius* (Moritz 1982b): M.11 (Fig. 6B); *Thrips* (Risler 1957): 14; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): k (Fig. 6A); *Caecilius* (ps): +; *Cerobasis* (ps): + (Fig. 16H); *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): 19 (Fig. 6D); *Hybophthirus* (Tröster 1990a): M25; *Pediculus* (ps): + (Figs. 25F,I, 26C); *Phthirus* (Hirsch 1986): M6;

Haematomyzus (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): M.38; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): 30a; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): M.38; *Perla* (Chisholm 1962): -

0hy8, M. praementosalivaris posterior

Systelloderes (Spangenberg et al. 2013b): ?; *Cryptostemma* (Spangenberg et al. 2013b): ?; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): ?; *Corixa* (Benwitz 1956): ?; *Gelastocoris* (Parsons 1959): ?; *Lethocerus* (Parsons 1968): ?; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): ?; *Gerris* (Spangenberg et al. 2013b): ?; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): ?; *Triatoma* (Barth 1952a,b, 1953a,b): ?; *Dysdercus* (Khan 1972): ?; *Hackeriella* (Spangenberg et al. 2013a): ?; *Hemiodoecus* (Singh 1971): ?; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): ?; *Macrosiphum* (Singh 1971): ?; *Dactylosphaera* (Rilling 1960): ?; *Trialeurodes* (Weber 1935): ?; *Aleurolobus* (Singh 1971): ?; *Aleyrodes* (ps): ?; *Psylla* (Weber 1929): ?; *Diaphorina* (Singh 1971): ?; *Cacopsylla* (ps): ?; *Pseudococcus* (ps): ?; *Perissopneumon* (Singh 1971): ?; *Tibicina* (Snodgrass 1927; Kramer 1950): ?; *Idiocerus* (Arora & Singh 1962): ?; *Philaenus* (ps): ?; *Lepyronia* (Kramer 1950): ?; *Platypleura* (Singh 1971): ?; *Oxyrhachis* (Singh 1971): ?; *Scolops* (Kramer 1950): ?; *Melicharia* (Singh 1971): ?; *Dictyophara* (ps): ?; *Aeolothrips fasciatus* (Mickoleit 1963): 23 (Fig. 6B); *Aeolothrips intermedius* (Moritz 1982b): M.10 (Fig. 6B); *Thrips* (Risler 1957): 13; *Haplothrips* (Mickoleit 1963): 23; *Phlaeothrips* (Mickoleit 1963): 23; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): j (Fig. 6A); *Caecilius* (ps): +; *Cerobasis* (ps): + (Fig. 16F); *Troctes* (Noland 1924): /; *Liposcelis* (ps): + (Fig. 18F); *Gliricola* (Risler & Geising 1965): 17; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): 18; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): Musc. ojator salivarii; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): M.39; *Osmylus* (Beutel et al. 2010): M39; *Schizodactylus* (Khattar 1964): 30b; *Oniscigaster* (Staniczek 2001): M49; *Zorotypus* (Beutel & Weide 2005): M.39; *Perla* (Chisholm 1962): -

0hy9, M. oralis transversalis

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): M16 (Fig. 7F); *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): tm; *Osmylus* (Beutel et al. 2010): M67; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): M.67 + tm; *Perla* (Chisholm 1962): -

0hy10, M. loroloralis

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): M24; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

0hy11, M. lorosalivarialis

absent in all taxa examined and not mentioned in other studes

0hy12, M. hypopharyngosalivaris

Systelloderes (Spangenberg et al. 2013b): M23; *Cryptostemma* (Spangenberg et al. 2013b): M23; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): KM25; *Corixa* (Benwitz 1956): retr pist; *Gelastocoris* (Parsons 1959): KM25; *Lethocerus* (Parsons 1968): H25; *Belostoma* (Verma et al. 1973): +; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): KM25; *Gerris* (Spangenberg et al. 2013b): M23; *Hydrometra* (Sprague 1956): +; *Saldula* (Parsons 1962): 25; *Triatoma* (Barth 1952a,b, 1953a,b): Mu12; *Dysdercus* (Khan 1972): DSS1+2; *Hackeriella* (Spangenberg et al. 2013a): M23 (Fig. 7E); *Hemiodoecus* (Singh 1971): 41; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): m. retr. pist2; *Macrosiphum* (Singh 1971): 41; *Dactylosphaera* (Rilling 1960): 6; *Trialeurodes* (Weber 1935): m. retr. pist.; *Aleurolobus* (Singh 1971): 41; *Aleyrodes* (ps): +; *Psylla* (Weber 1929): m. retr. pist.; *Diaphorina* (Singh 1971): 41; *Cacopsylla* (ps): +; *Pseudococcus* (ps): + (Fig. 11C); *Perissopneumon* (Singh 1971): 41; *Tibicina* (Snodgrass 1927; Kramer 1950): dsyr; *Idiocerus* (Arora & Singh 1962): 32; *Philaenus* (ps): +; *Lepyronia* (Kramer 1950): dsyr; *Platypleura* (Singh 1971): 41; *Oxyrhachis* (Singh 1971): 41; *Scolops* (Kramer 1950): dsyr; *Melicharia* (Singh 1971): 41; *Dictyophara* (ps): +; *Aeolothrips fasciatus* (Mickoleit 1963): 28 (Fig. 7D); *Aeolothrips intermedius* (Moritz 1982b): M.14 (Fig. 7D); *Thrips* (Risler 1957): 17; *Haplothrips* (Mickoleit 1963): 28; *Phlaeothrips* (Mickoleit 1963): 28; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): m (Fig. 7A); *Caecilius* (ps): +; *Cerobasis* (ps): + (Fig. 7B); *Troctes* (Noland 1924): /; *Liposcelis* (ps): +; *Gliricola* (Risler & Geising 1965): 10; *Myrsidea* (Buckup 1959): 24; *Pseudomenopon* (Haub 1967): 24; *Piagetiella* (ps): + (Fig. 20F); *Trochiloecetes* (Haub 1983): 3.4.2.; *Trimenopon* (Stöwe 1943): ms; *Bovicola* (Risler 1951): 21; *Ornithobius* (Haub 1971): 5.1.1.; *Columbicola* (ps): + (Fig. 7C); *Haematopinus* (Ramcke 1965): ? (Ramcke [1965] emphasized the absence of “Musc. salivarii”, but assumed that the muscle fibres mesad the hypopharyngeal wall are likely homologous with “M. hypopharyngosalivaris”.); *Hybophthirus* (Tröster 1990a): M32 (Fig. 7F); *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): 8; *Macroxyela* (Beutel & Vilhelmsen 2007): M.37;

Osmylus (Beutel et al. 2010): M37; *Schizodactylus* (Khattar 1964): 29; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): M.37; *Perla* (Chisholm 1962): H. COM.

0hy13, M. annularis salivarii

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): 29; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): 29; *Phlaeothrips* (Mickoleit 1963): 29; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): M.40; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): M.40; *Perla* (Chisholm 1962): -

0hyx1, "M. protractor hypopharyngis"

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): 25 (Fig. 7D); *Aeolothrips intermedius* (Moritz 1982b): M.12 (Fig. 7D); *Thrips* (Risler 1957): 15; *Haplothrips* (Mickoleit 1963): 25; *Phlaeothrips* (Mickoleit 1963): 25; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): h (Figs. 6A, 7A); *Caecilius* (ps): +; *Cerobasis* (ps): + (Figs. 7B, 16G); *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): 12; *Myrsidea* (Buckup 1959): 23; *Pseudomenopon* (Haub 1967): 23; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): 2.4.2.3.; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): 19; *Ornithobius* (Haub 1971): 4.4.1.6.; *Columbicola* (ps): + (Figs. 7C, 22F); *Haematopinus* (Ramcke 1965): 16 (Fig. 6D); *Hybophthirus* (Tröster 1990a): M31 (Fig. 7F); *Pediculus* (ps): + (Figs. 25H,I); *Phthirus* (Hirsch 1986): M10; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

0hyx2, tentorial ligament

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): ligament fibreux tentorio-hypopharyngien (Fig. 7A); *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): Tentorialligament; *Pseudomenopon* (Haub 1967): Tentorialligament; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): lig. tentorio hypopharyngien; *Ornithobius* (Haub 1971): Tentoriooraligament (Haub [1976] originally used the term "Tentorio-Oralligament" for the connection between the anterior tentorial arms and the dorsolateral edge of the cibarial sclerite, but the "Tentorialigament" connects in fact the corpotentorium and the posterior cibarial sclerite. In Haub [1971] the "Tentoriooraligament" of *Ornithobius* is described as a connection between the corpotentorium and the cibarial sclerite. This ligament is probably unpaired in *Ornithobius* and also in *Bovicola* [Haub 1971]. In *Bovicola*, however, only a ligament between the corpotentorium and cibarial sclerite is present (Risler 1951). Consequently, the "Tentoriooralligament" of Haub [1971] is probably equivalent with the "Tentorialligament" of Haub [1967]); *Columbicola* (ps): + (Fig. 7C); *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

0hyx3, muscle of hypopharyngeal wing in Hemiptera

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): 46; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus*

(Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

0hyx4, "M. hypopharyngo salivaris secundus"
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): M24 (Fig. 7E); *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): m. dil. cup1 (In contrast to Spangenberg et al. [2013a] and based on a more extensive taxon sampling this homology interpretation is accepted here. It implies a shift of the insertion to the puming chamber); *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): 7; *Trialeurodes* (Weber 1935): m. cup; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): +; *Psylla* (Weber 1929): m. dil. cup.; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): +; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): 9; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

0hyx5, "M. hypopharyngo salivaris tertius"
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): m. retr. pist1; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): 5; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -;

Schizodactylus (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

0hyx6, "M. hypopharyngo salivaris quartus"
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): m. dil. cup2; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

0hyx7, "M. hypopharyngo salivaris quintus"
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): m. dil. cup3+4; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): 8; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

0hyx8, "M. hypopharyngo salivaris sextus"
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): m. dil. cup5; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

0hyx9, "Msusph"
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): Msusph; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

0hyx10, "M. intersalivarius"
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et

al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): 30; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

0hyx11, "M. salivarii longitudinales"
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): 7; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

0hyx12, "M. hypopharyngo salivaris septus"
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al.

2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): -; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): 36; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

Muscles of the tentorium

absent in all taxa examined and not mentioned in other studies

Muscles of the cibarium

0ci1, M. clypeopalatalis

Systelloderes (Spangenberg et al. 2013b): M25; *Cryptostemma* (Spangenberg et al. 2013b): M25; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): KM14; *Corixa* (Benwitz 1956): abd lr; *Gelastocoris* (Parsons 1959): KM14; *Lethocerus* (Parsons 1968): H14; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): KM14; *Gerris* (Spangenberg et al. 2013b): M25; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): 14; *Triatoma* (Barth 1952a,b, 1953a,b): Mu1; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): M25; *Hemiodoecus* (Singh 1971): 31; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): m. dil1; *Macrosiphum* (Singh 1971): 31; *Dactylosphaera* (Rilling 1960): 1; *Trialeurodes* (Weber 1935): m. dil.; *Aleurolobus* (Singh 1971): 31; *Aleyrodes* (ps): +; *Psylla* (Weber 1929): m. dil.; *Diaphorina* (Singh 1971): 31; *Cacopsylla* (ps): +; *Pseudococcus* (ps): +; *Perissopneumon* (Singh 1971): 31; *Tibicina* (Snodgrass 1927; Kramer 1950): +; *Idiocerus* (Arora & Singh 1962): 22; *Philaenus* (ps): + (Figs. 13A,B); *Lepyronia* (Kramer 1950): - (compare fig. 18 with fig. 30 of Kramer (1950)); *Platypleura* (Singh 1971): 31; *Oxyrhachis* (Singh 1971): 31; *Scolops* (Kramer 1950): +; *Melicharia* (Singh 1971): 31; *Dictyophara* (ps): +; *Aeolothrips fasciatus* (Mickoleit 1963): 31; *Aeolothrips intermedius* (Moritz 1982b): M.7; *Thrips* (Risler 1957): 22; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): A'; *Caecilius* (ps): +; *Cerobasis* (ps): + (Fig. 16B); *Troctes* (Noland 1924): /; *Liposcelis* (ps): +; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Buckup 1959): 30; *Pseudomenopon* (Haub 1967): 30; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): 3.2.2.3.1.; *Trimenopon* (Stöwe 1943): A'; *Bovicola* (Risler 1951): 28; *Ornithobius* (Haub 1971): 7.2.1.1.; *Columbicola* (ps): + (Figs. 22B,C,D) *Haematopinus* (Ramcke 1965): 3a-d; *Hybophthirus* (Tröster 1990a): M8; *Pediculus* (ps): + (Figs. 25D,E); *Phthirus* (Hirsch 1986): M15-M18; *Haematomyzus* (Weber 1969): 11-13; *Macroxyela* (Beutel & Vilhelmsen 2007): M.43a,c; *Osmylus* (Beutel et al. 2010): M43; *Schizodactylus* (Khattar 1964): 37; *Oniscigaster* (Staniczek 2001): M11; *Zorotypus* (Beutel & Weide 2005): M.43; *Perla* (Chisholm 1962): A. OES. DIL.

Muscles of the bucca

0bu1, M. clypeobuccalis

Systelloderes (Spangenberg et al. 2013b): M26; *Cryptostemma* (Spangenberg et al. 2013b): M26; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): KM15; *Corixa*

(Benwitz 1956): dil cib; *Gelastocoris* (Parsons 1959): KM15; *Lethocerus* (Parsons 1968): H15; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): KM15; *Gerris* (Spangenberg et al. 2013b): M26; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): Mu2; *Dysdercus* (Khan 1972): DSP1; *Hackeriella* (Spangenberg et al. 2013a): M26; *Hemiodoecus* (Singh 1971): 33; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): m. dil2; *Macrosiphum* (Singh 1971): 33; *Dactylosphaera* (Rilling 1960): 2; *Trialeurodes* (Weber 1935): m. dil.; *Aleurolobus* (Singh 1971): 33; *Aleyrodes* (ps): +; *Psylla* (Weber 1929): m. dil.; *Diaphorina* (Singh 1971): 33; *Cacopsylla* (ps): +; *Pseudococcus* (ps): + (Figs. 10D,E); *Perissopneumon* (Singh 1971): 33; *Tibicina* (Snodgrass 1927; Kramer 1950): dlclp; *Idiocerus* (Arora & Singh 1962): 24; *Philaenus* (ps): +; *Lepyronia* (Kramer 1950): dlclp; *Platypleura* (Singh 1971): 33; *Oxyrhachis* (Singh 1971): 33; *Scolops* (Kramer 1950): dlclp; *Melicharia* (Singh 1971): 33; *Dictyophara* (ps): +; *Aeolothrips fasciatus* (Mickoleit 1963): 34; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): A; *Caecilius* (ps): +; *Cerobasis* (ps): + (Fig. 16B); *Troctes* (Noland 1924): l. m.; *Liposcelis* (ps): + (Fig. 18B); *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Buckup 1959): 31-33; *Pseudomenopon* (Haub 1967): 31-33; *Piagetiella* (ps): + (Figs. 20B,C); *Trochiloecetes* (Haub 1983): 3.2.2.3.2. + 3.2.2.3.3.; *Trimenopon* (Stöwe 1943): A; *Bovicola* (Risler 1951): 29-31; *Ornithobius* (Haub 1971): 7.2.1.2.-7.2.1.3.; *Columbicola* (ps): + (Figs. 22D,E); *Haematopinus* (Ramcke 1965): 3e-f; *Hybophthirus* (Tröster 1990a): M9; *Pediculus* (ps): + (Figs. 25D,E); *Phthirus* (Hirsch 1986): M15-M18; *Haematomyzus* (Weber 1969): 14 + 15; *Macroxyela* (Beutel & Vilhelmsen 2007): M.44; *Osmylus* (Beutel et al. 2010): M44; *Schizodactylus* (Khattar 1964): 38; *Oniscigaster* (Staniczek 2001): M12-M14; *Zorotypus* (Beutel & Weide 2005): ? ("M. clypeobuccalis (M.44) – probably absent; it cannot be fully excluded that M. clypeobuccalis is represented by the posteriormost bundle of M. clypeopalatalis b (M. 43b); however, this appears rather unlikely as this is a very compact group of muscles" [Beutel & Weide 2005]); *Perla* (Chisholm 1962): -

0bu2, M. frontobuccalis anterior

Systelloderes (Spangenberg et al. 2013b): M27; *Cryptostemma* (Spangenberg et al. 2013b): M27; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): KM16; *Corixa* (Benwitz 1956): dil buc; *Gelastocoris* (Parsons 1959): KM16; *Lethocerus* (Parsons 1968): H16; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): KM16; *Gerris* (Spangenberg et al. 2013b): M27; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): 16; *Triatoma* (Barth 1952a,b, 1953a,b): Mu2; *Dysdercus* (Khan 1972): DSP2; *Hackeriella* (Spangenberg et al. 2013a): M27; *Hemiodoecus* (Singh 1971): 34; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): m. dil3; *Macrosiphum* (Singh 1971): 34; *Dactylosphaera* (Rilling 1960): 3; *Trialeurodes* (Weber 1935): m. dil.; *Aleurolobus* (Singh 1971): 34; *Aleyrodes* (ps): +; *Psylla* (Weber 1929): m. dil.; *Diaphorina* (Singh 1971): 34; *Cacopsylla* (ps): +; *Pseudococcus* (ps): + (Fig. 11A); *Perissopneumon* (Singh 1971): 34; *Tibicina* (Snodgrass 1927; Kramer 1950): dlclp; *Idiocerus* (Arora & Singh 1962): 25-27; *Philaenus* (ps): +; *Lepyronia* (Kramer 1950): dlclp; *Platypleura* (Singh 1971): 34; *Oxyrhachis* (Singh 1971): 34; *Scolops* (Kramer 1950): dlclp; *Melicharia* (Singh 1971): 34; *Dictyophara* (ps): +; *Aeolothrips fasciatus* (Mickoleit 1963): 32; *Aeolothrips intermedius* (Moritz 1982b): M.8; *Thrips* (Risler 1957): 23; *Haplothrips* (Mickoleit 1963): 32; *Phlaeothrips* (Mickoleit 1963): 32; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): B; *Caecilius* (ps): +; *Cerobasis* (ps): + (Fig. 16B); *Troctes* (Noland 1924): /; *Liposcelis* (ps): + (Figs. 18B,C); *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Buckup 1959): 34 + 36; *Pseudomenopon* (Haub 1967): 36; *Piagetiella* (ps): + (Fig. 20C); *Trochiloecetes* (Haub 1983): 3.2.2.2.; *Trimenopon* (Stöwe 1943): B1 + B2; *Bovicola* (Risler 1951): 34; *Ornithobius* (Haub 1971): 7.2.1.7.; *Columbicola* (ps): + (Figs. 22D,E,F); *Haematopinus* (Ramcke 1965): 3e-f; *Hybophthirus* (Tröster 1990a): M10; *Pediculus* (ps): + (Fig. 25E); *Phthirus* (Hirsch 1986): M19; *Haematomyzus* (Weber 1969): 16; *Macroxyela* (Beutel & Vilhelmsen 2007): M.45; *Osmylus* (Beutel et al. 2010): M45; *Schizodactylus* (Khattar 1964): 39 + 40; *Oniscigaster* (Staniczek 2001): M15; *Zorotypus* (Beutel & Weide 2005): M.45; *Perla* (Chisholm 1962): M. OES. DIL.

0bu3, M. frontobuccalis posterior
Systelloderes (Spangenberg et al. 2013b): M30; *Cryptostemma* (Spangenberg et al. 2013b): M30; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): KM17 + KM17a; *Corixa* (Benwitz 1956): dil ph1 + dil ph2 + m dilatator oris; *Gelastocoris* (Parsons 1959): KM17 + KM17a; *Lethocerus* (Parsons 1968): H17 + H17a; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): KM17 + KM17a; *Gerris* (Spangenberg et al. 2013b): M30; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): 17a; *Triatoma* (Barth 1952a,b, 1953a,b): Mu3; *Dysdercus* (Khan 1972): DPH; *Hackeriella* (Spangenberg et al. 2013a): M30; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): 4; *Trialeurodes* (Weber 1935): ?; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): +; *Psylla* (Weber 1929): ?; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): +; *Pseudococcus* (ps): +; *Perissopneumon* (Singh 1971): “few and very fine muscle fibres”; *Tibicina* (Snodgrass 1927; Kramer 1950): dlclp; *Idiocerus* (Arora & Singh 1962): 27; *Philaenus* (ps): +; *Lepyronia* (Kramer 1950): dlclp; *Platypleura* (Singh 1971): 35 + 36; *Oxyrhachis* (Singh 1971): 35 + 36; *Scolops* (Kramer 1950): dlclp; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): +; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): 24; *Haplothrips* (Mickoleit 1963): 33; *Phlaeothrips* (Mickoleit 1963): 33; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): E1 + E2; *Caecilius* (ps): +; *Cerobasis* (ps): + (Fig. 16B); *Troctes* (Noland 1924): /; *Liposcelis* (ps): + (Figs. 18D,E); *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Buckup 1959): 37; *Pseudomenopon* (Haub 1967): 38; *Piagetiella* (ps): + (Figs. 20C,D); *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): b1 + b2; *Bovicola* (Risler 1951): 40; *Ornithobius* (Haub 1971): 8.1.1.; *Columbicola* (ps): + (Fig. 22F); *Haematopinus* (Ramcke 1965): 7a + 7b; *Hybophthirus* (Tröster 1990a): M13; *Pediculus* (ps): + (Fig. 25F); *Phthirus* (Hirsch 1986): M22; *Haematomyzus* (Weber 1969): 19; *Macroxyela* (Beutel & Vilhelmsen 2007): M.46; *Osmylus* (Beutel et al. 2010): M46; *Schizodactylus* (Khattar 1964): 41; *Oniscigaster* (Staniczek 2001): M16; *Zorotypus* (Beutel & Weide 2005): M.46; *Perla* (Chisholm 1962): P. OES. DIL.

0bu4, M. tentoriobuccalis lateralis
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): -; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): M20; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

0bu5, M. tentoriobuccalis anterior

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): KM18; *Corixa* (Benwitz 1956): dil ph3 v; *Gelastocoris* (Parsons 1959): KM18; *Lethocerus* (Parsons 1968): H18; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): 18; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): M29; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): m. depr. phar; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): Ligamente; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): m. depr. phar; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): +; *Pseudococcus* (ps): + (Figs. 10D,E, 11A); *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): second pair of pharyngeal dilatators; *Idiocerus* (Arora & Singh 1962): 28; *Philaenus* (ps): +; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): 39; *Oxyrhachis* (Singh 1971): 39; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): 39; *Dictyophara* (ps): +; *Aeolothrips fasciatus* (Mickoleit 1963): 33; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): z + x + y + u + v; *Caecilius* (ps): +; *Cerobasis* (ps): + (Figs. 16D,E); *Troctes* (Noland 1924): /; *Liposcelis* (ps): + (Fig. 18H); *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Buckup 1959): 47-49; *Pseudomenopon* (Haub 1967): 49-51; *Piagetiella* (ps): + (Figs. 20F,G); *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): z + x + y + u + w; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): M50; *Schizodactylus* (Khattar 1964): 45; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

0bu6, M. tentoriobuccalis posterior

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Buckup 1959): 44 + 45; *Pseudomenopon* (Haub 1967): 46 + 47; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): -; *Ornithobius* (Haub 1971): 8.1.7. + 8.1.8.; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): 18; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): M48; *Schizodactylus* (Khattar 1964): 46-48; *Oniscigaster* (Staniczek 2001): M21; *Zorotypus* (Beutel & Weide 2005): M.50; *Perla* (Chisholm 1962): -

0bux1, "M. frontobuccalis anterior secundus"
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,ba, b, 1953a, b): -; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): first pair of pharyngeal dilatator muscles, phym1; *Idiocerus* (Arora & Singh 1962): 29; *Philaenus* (ps): +; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): 40; *Aeolothrips intermedius* (Moritz 1982b): M.16; *Thrips* (Risler 1957): 29; *Haplothrips* (Mickoleit 1963): 40; *Phlaeothrips* (Mickoleit 1963): 40; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): F; *Caecilius* (ps): +; *Cerobasis* (ps): + (Figs. 16B,C); *Troctes* (Noland 1924): /; *Liposcelis* (ps): + (Figs. 18C,E); *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Buckup 1959): 36; *Pseudomenopon* (Haub 1967): 37; *Piagetiella* (ps): + (Figs. 20E,F); *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): 35 + 36; *Ornithobius* (Haub 1971): 8.1.3.; *Columbicola* (ps): +; *Haematopinus* (Ramcke 1965): 7c; *Hybophthirus* (Tröster 1990a): M14; *Pediculus* (ps): +; *Phthirus* (Hirsch 1986): M23; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): 44; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

Muscles of the pharynx

0ph1, M. verticopharyngealis
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): KM19; *Corixa* (Benwitz 1956): dil ph3 d; *Gelastocoris* (Parsons 1959): KM19; *Lethocerus* (Parsons 1968): H19; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): 19; *Triatoma* (Barth 1952a,b, 1953a,b): Mu17; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): M28; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): 38; *Cacopsylla* (ps): -; *Pseudococcus* (ps): +; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): third pair of pharyngeal dilatators; *Idiocerus* (Arora & Singh 1962): 31; *Philaenus* (ps): +; *Lepyronia* (Kramer 1950): phmy1; *Platypleura* (Singh 1971): 38; *Oxyrhachis* (Singh 1971): 38; *Scolops* (Kramer 1950): + (see fig. 13); *Melicharia* (Singh 1971): 38; *Dictyophara* (ps): +; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): H; *Caecilius* (ps): +; *Cerobasis* (ps): + (Fig. 16C); *Troctes* (Noland 1924): /; *Liposcelis* (ps): + (Figs. 18H,I); *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Buckup 1959): 38; *Pseudomenopon* (Haub 1967): 39; *Piagetiella* (ps): + (Figs. 20G,H); *Trochiloecetes* (Haub 1983): 3.5.2.1.; *Trimenopon* (Stöwe 1943): G + H; *Bovicola* (Risler 1951): 40; *Ornithobius* (Haub 1971): 8.1.2.; *Columbicola* (ps): +; *Haematopinus* (Ramcke 1965): 9; *Hybophthirus* (Tröster 1990a): Haltemuskel des Pharynx; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): 20; *Macroxyela* (Beutel & Vilhelmsen 2007): M.51; *Osmylus* (Beutel et al. 2010): M51; *Schizodactylus* (Khattar 1964): 42; *Oniscigaster* (Staniczek 2001): M17; *Zorotypus* (Beutel & Weide 2005): M.51; *Perla* (Chisholm 1962): -

0ph2, M. tentoriopharyngealis
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): 40; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): fifth pair of pharyngeal dilatator muscles; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): +; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): 40; *Oxyrhachis* (Singh 1971): 40; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): 40; *Dictyophara* (ps): +; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Buckup 1959): 46; *Pseudomenopon* (Haub 1967): 48; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): 3.5.2.4.; *Trimenopon* (Stöwe 1943): s; *Bovicola* (Risler 1951): 41; *Ornithobius* (Haub 1971): -; *Columbicola* (ps): +; *Haematopinus* (Ramcke 1965): + (see Tröster (1990a) p. 60); *Hybophthirus* (Tröster 1990a): M12 (several subdivisions of pharyngeal muscles impede the homologization. The interpretation presented her differs from Tröster [1990a], who homologized M12 of *Hybophthirus* with M. posterior sitophori of *Pseudomenopon* [Haub 1967], *Myrsidea* [Buckup 1959], *Bovicola* [Risler 1951], and *Ornithobius* [Haub 1971]. In these species the muscle inserts on the oral hypopharyngeal arm and not on the anatomical mouth opening. The homology of M12 of *Hybophthirus* with the muscles z,x,y,u,v of *Stenopsocus* [Badonnel 1934] is also rejected as the latter originate on the anterior tentorial arms and not on the posterior ones as in the aardvark louse); *Pediculus* (ps): + (Fig. 25F); *Phthirus* (Hirsch 1986): M24; *Haematomyzus* (Weber 1969): 21; *Macroxyela* (Beutel & Vilhelmsen 2007): M.52; *Osmylus* (Beutel et al. 2010): M52; *Schizodactylus* (Khattar 1964): 49 + 50; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): M.52; *Perla* (Chisholm 1962): -

0ph3, M. postoccipitopharyngealis
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): fourth pair of pharyngeal dilatator muscles; *Idiocerus* (Arora & Singh 1962): 30; *Philaenus* (ps): +; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): 37; *Oxyrhachis* (Singh 1971): 37; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Buckup 1959): 50; *Pseudomenopon* (Haub 1967): 52; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): m. radialis pharyngis lateralis 2; *Trimenopon* (Stöwe 1943): t; *Bovicola* (Risler 1951): 42; *Ornithobius* (Haub 1971): 8.1.9.; *Columbicola* (ps): -; *Haematopinus* (Ramcke 1965): 8a-c; *Hybophthirus* (Tröster 1990a): M15; *Pediculus* (ps): + (Fig. 25F); *Phthirus* (Hirsch 1986): M25;

Haematomyzus (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

0phx1, "M. sitophori pharyngis"
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): -; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): -; *Idiocerus* (Arora & Singh 1962): -; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): -; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): -; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): -; *Aeolothrips intermedius* (Moritz 1982b): -; *Thrips* (Risler 1957): -; *Haplothrips* (Mickoleit 1963): -; *Phlaeothrips* (Mickoleit 1963): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Buckup 1959): -; *Pseudomenopon* (Haub 1967): -; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): -; *Trimenopon* (Stöwe 1943): -; *Bovicola* (Risler 1951): 23 + 24; *Ornithobius* (Haub 1971): 6.1.4.; *Columbicola* (ps): + (Fig. 7C); *Haematopinus* (Ramcke 1965): -; *Hybophthirus* (Tröster 1990a): längsverlaufendes Muskelpaar (see Tröster (1990a) p. 61) (Fig. 7F); *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Beutel & Vilhelmsen 2007): -; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): -; *Oniscigaster* (Staniczek 2001): -; *Zorotypus* (Beutel & Weide 2005): -; *Perla* (Chisholm 1962): -

Muscles of the stomadeum

0st1, M. annularis stomodaei
Systelloderes (Spangenberg et al. 2013b): +; *Cryptostemma* (Spangenberg et al. 2013b): +; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): RM; *Corixa* (Benwitz 1956): con ph; *Gelastocoris* (Parsons 1959): /; *Lethocerus* (Parsons 1968): /; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): +; *Gerris* (Spangenberg et al. 2013b): +; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): /; *Triatoma* (Barth 1952a,b, 1953a,b): MUR; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): /; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): /; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): Ringmuskulatur; *Aleurolobus* (Singh 1971): /; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): /; *Cacopsylla* (ps): +; *Pseudococcus* (ps): +; *Perissopneumon* (Singh 1971): /; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): /; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): /; *Platypleura* (Singh 1971): /; *Oxyrhachis* (Singh 1971): /; *Scolops* (Kramer 1950): /; *Melicharia* (Singh 1971): /; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): 36 + 37; *Aeolothrips intermedius* (Moritz 1982b): +; *Thrips* (Risler 1957): 25-27; *Haplothrips* (Mickoleit 1963): 36 + 37 + 39; *Phlaeothrips* (Mickoleit 1963): 36 + 37 + 39; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): muscles circulaires; *Caecilius* (ps): +; *Cerobasis* (ps): +; *Troctes* (Noland 1924): +; *Liposcelis* (ps): +; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Buckup 1959): 42 + 43; *Pseudomenopon* (Haub 1967): 44 + 45; *Piagetiella* (ps): +; *Trochiloecetes* (Haub 1983): 3.5.2.3.; *Trimenopon* (Stöwe 1943): M. circ.; *Bovicola* (Risler 1951): 39; *Ornithobius* (Haub 1971): 8.1.6.; *Columbicola* (ps): +; *Haematopinus* (Ramcke 1965): Wandmuskulatur des Pharynx; *Hybophthirus* (Tröster 1990a): M18; *Pediculus* (ps): +;

Phthirus (Hirsch 1986): quer- und schrägverlaufende Ringmuskel; *Haematomyzus* (Weber 1969): 22; *Macroxyela* (Beutel & Vilhelmsen 2007): M.68; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): +; *Oniscigaster* (Staniczek 2001): M10; *Zorotypus* (Beutel & Weide 2005): M.68; *Perla* (Chisholm 1962): thick band of circular muscles

0st2, M. longitudinalis stomodaei

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1959): /; *Lethocerus* (Parsons 1968): /; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): /; *Saldula* (Parsons 1962): /; *Triatoma* (Barth 1952a,b, 1953a,b): -; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): /; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): /; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): /; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): /; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): /; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): /; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): /; *Platypleura* (Singh 1971): /; *Oxyrhachis* (Singh 1971): /; *Scolops* (Kramer 1950): /; *Melicharia* (Singh 1971): /; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): 38; *Aeolothrips intermedius* (Moritz 1982b): M.15; *Thrips* (Risler 1957): 28; *Haplothrips* (Mickoleit 1963): 38; *Phlaeothrips* (Mickoleit 1963): 38; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): muscles longitudinaux; *Caecilius* (ps): +; *Cerobasis* (ps): +; *Troctes* (Noland 1924): +; *Liposcelis* (ps): ?; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Buckup 1959): 39-41; *Pseudomenopon* (Haub 1967): 40-43; *Piagetiella* (ps): +; *Trochiloecetes* (Haub 1983): 3.5.2.2.; *Trimenopon* (Stöwe 1943): M + N; *Bovicola* (Risler 1951): 37 + 38; *Ornithobius* (Haub 1971): 8.1.4. + 8.1.5.; *Columbicola* (ps): +; *Haematopinus* (Ramcke 1965): Wandmuskulatur des Pharynx; *Hybophthirus* (Tröster 1990a): M17; *Pediculus* (ps): +; *Phthirus* (Hirsch 1986): -; *Haematomyzus* (Weber 1969): 23; *Macroxyela* (Beutel & Vilhelmsen 2007): M.69; *Osmylus* (Beutel et al. 2010): -; *Schizodactylus* (Khattar 1964): +; *Oniscigaster* (Staniczek 2001): M9; *Zorotypus* (Beutel & Weide 2005): M.69; *Perla* (Chisholm 1962): -

Dorsal longitudinal extrinsic head muscles

ldlm1, M. prophragma-occipitalis

Systelloderes (Spangenberg et al. 2013b): M2; *Cryptostemma* (Spangenberg et al. 2013b): M2; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): TM3; *Corixa* (Benwitz 1956): retr cap2; *Gelastocoris* (Parsons 1960a): TM3; *Lethocerus* (Parsons 1968): 3; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): M2; *Hydrometra* (Sprague 1956): M3; *Saldula* (Parsons 1963): 3; *Triatoma* (Barth 1952a,b, 1953a,b): /; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): M2; *Hemiodoecus* (Singh 1971): 47; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): 47; *Dactylosphaera* (Rilling 1960): 65 +66; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): 47; *Aleyrodes* (ps): +; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): 47; *Cacopsylla* (ps): +; *Pseudococcus* (ps): +; *Perissopneumon* (Singh 1971): 47; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): /; *Philaenus* (ps): +; *Lepyronia* (Kramer 1950): /; *Platypleura* (Singh 1971): 47; *Oxyrhachis* (Singh 1971): 47; *Scolops* (Kramer 1950): /; *Melicharia* (Singh 1971): 47; *Dictyophara* (ps): +; *Aeolothrips fasciatus* (Mickoleit 1963): /; *Aeolothrips intermedius* (Moritz 1982c): M.29; *Thrips* (Mickoleit 1961): M. lev. cap. prphr.; *Haplothrips* (Mickoleit 1961): M. lev. cap. prphr.; *Phlaeothrips* (Mickoleit 1961): M. lev. cap. prphr.; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): Dpo; *Caecilius* (ps): +; *Cerobasis* (ps): + (Figs. 16F,G,H); *Troctes* (Noland 1924): /; *Liposcelis* (ps): +; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Mayer 1954): I dlm1; *Pseudomenopon* (Haub 1967): /; *Piagetiella* (ps): +; *Trochiloecetes* (Haub 1983): /; *Trimenopon* (Mayer 1954): I dlm1; *Bovicola* (Mayer 1954): I dlm1; *Ornithobius* (Haub 1971): /;

Columbicola (ps): + (Fig. 22H); *Haematopinus* (Tröster 1997): M1; *Hybophthirus* (Tröster 1997): M1; *Pediculus* (ps): + (Fig. 25J); *Phthirus* (Hirsch 1986): /; *Haematomyzus* (Weber 1969): 28; *Macroxyela* (Vilhelmsen 2000): 4; *Osmylus* (Beutel et al. 2010): /; *Schizodactylus* (Khattar 1964): /; *Oniscigaster* (Staniczek 2001): /; *Zorotypus* (Friedrich & Beutel 2008): Idlm1; *Perla* (Chisholm 1962): No.15 + No.16

Idlm2, M. pronoto-occipitalis
Systelloderes (Spangenberg et al. 2013b): M1a; *Cryptostemma* (Spangenberg et al. 2013b): M1a; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): TM1; *Corixa* (Benwitz 1956): retr cap1; *Gelastocoris* (Parsons 1960a): TM1; *Lethocerus* (Parsons 1968): 1; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): ? (second cranial flexor); *Gerris* (Spangenberg et al. 2013b): M1a; *Hydrometra* (Sprague 1956): M2; *Saldula* (Parsons 1963): 1; *Triatoma* (Barth 1952a,b, 1953a,b): /; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): M1a; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): Odlm; *Macrosiphum* (Singh 1971): 42; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): Odlm; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): +; *Psylla* (Weber 1929): Odlm2; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): +; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): 42; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): /; *Philaenus* (ps): +; *Lepyronia* (Kramer 1950): /; *Platypleura* (Singh 1971): 42; *Oxyrhachis* (Singh 1971): 42; *Scolops* (Kramer 1950): /; *Melicharia* (Singh 1971): 42; *Dictyophara* (ps): +; *Aeolothrips fasciatus* (Mickoleit 1963): /; *Aeolothrips intermedius* (Moritz 1982c): M.30; *Thrips* (Mickoleit 1961): M. lev. cap. terg.; *Haplothrips* (Mickoleit 1961): M. lev. cap. terg.; *Phlaeothrips* (Mickoleit 1961): M. lev. cap. terg.; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): muscles protergo-occipitaux obliques; *Caecilius* (ps): +; *Cerobasis* (ps): + (Fig. 16H); *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Mayer 1954): I dlm2; *Pseudomenopon* (Haub 1967): /; *Piagetiella* (ps): +; *Trochiloecetes* (Haub 1983): /; *Trimenopon* (Mayer 1954): I dlm2; *Bovicola* (Mayer 1954): -; *Ornithobius* (Haub 1971): /; *Columbicola* (ps): -; *Haematopinus* (Tröster 1997): -; *Hybophthirus* (Tröster 1997): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): /; *Haematomyzus* (Weber 1969): ? (26); *Macroxyela* (Vilhelmsen 2000): -; *Osmylus* (Beutel et al. 2010): /; *Schizodactylus* (Khattar 1964): /; *Oniscigaster* (Staniczek 2001): /; *Zorotypus* (Friedrich & Beutel 2008): Idlm2; *Perla* (Chisholm 1962): No.6 + No.9

Idlm3, M. prophragma-cervicalis
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1960a): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1963): -; *Triatoma* (Barth 1952a,b, 1953a,b): /; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): /; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): /; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): /; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): /; *Aeolothrips intermedius* (Moritz 1982c): -; *Thrips* (Mickoleit 1961): -; *Haplothrips* (Mickoleit 1961): -; *Phlaeothrips* (Mickoleit 1961): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Mayer 1954): -; *Pseudomenopon* (Haub 1967): /; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): /; *Trimenopon* (Mayer 1954): -; *Bovicola* (Mayer 1954): -; *Ornithobius* (Haub 1971): /; *Columbicola* (ps): -; *Haematopinus* (Tröster 1997): -; *Hybophthirus* (Tröster 1997): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): /; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Vilhelmsen 2000): 8; *Osmylus* (Beutel et al. 2010): /; *Schizodactylus*

(Khattar 1964): /; *Oniscigaster* (Staniczek 2001): /; *Zorotypus* (Friedrich & Beutel 2008): Idlm3; *Perla* (Chisholm 1962): No.17

Idlm4, M. cervico-occipitalis dorsalis
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1960a): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1963): -; *Triatoma* (Barth 1952a,b, 1953a,b): /; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): /; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): /; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): /; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): /; *Aeolothrips intermedius* (Moritz 1982c): -; *Thrips* (Mickoleit 1961): -; *Haplothrips* (Mickoleit 1961): -; *Phlaeothrips* (Mickoleit 1961): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Mayer 1954): -; *Pseudomenopon* (Haub 1967): /; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): /; *Trimenopon* (Mayer 1954): -; *Bovicola* (Mayer 1954): -; *Ornithobius* (Haub 1971): /; *Columbicola* (ps): -; *Haematopinus* (Tröster 1997): -; *Hybophthirus* (Tröster 1997): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): /; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Vilhelmsen 2000): -; *Osmylus* (Beutel et al. 2010): /; *Schizodactylus* (Khattar 1964): /; *Oniscigaster* (Staniczek 2001): /; *Zorotypus* (Friedrich & Beutel 2008): Idlm4; *Perla* (Chisholm 1962): -

Dorsoventral extrinsic head muscles

Idvm1, M. cervico-occipitalis anterior
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1960a): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1963): -; *Triatoma* (Barth 1952a,b, 1953a,b): /; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): /; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): /; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): /; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): /; *Aeolothrips intermedius* (Moritz 1982c): M.31; *Thrips* (Mickoleit 1961): -; *Haplothrips* (Mickoleit 1961): M. compr. occ; *Phlaeothrips* (Mickoleit 1961): M. compr. occ; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): DVA; *Caecilius* (ps): +; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Mayer 1954): -; *Pseudomenopon* (Haub 1967): /; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): /; *Trimenopon* (Mayer 1954): -; *Bovicola* (Mayer 1954): -; *Ornithobius* (Haub 1971): /; *Columbicola* (ps): -; *Haematopinus* (Tröster 1997): -; *Hybophthirus* (Tröster 1997): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): /; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Vilhelmsen 2000): -; *Osmylus* (Beutel et al. 2010): /; *Schizodactylus* (Khattar 1964): /; *Oniscigaster* (Staniczek 2001): /; *Zorotypus* (Friedrich & Beutel 2008): Idvm1; *Perla* (Chisholm 1962): No.10

ldvm2, M. cervico-occipitalis medialis
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1960a): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1963): -; *Triatoma* (Barth 1952a,b, 1953a,b): /; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): /; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): /; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): /; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): /; *Aeolothrips intermedius* (Moritz 1982c): -; *Thrips* (Mickoleit 1961): -; *Haplothrips* (Mickoleit 1961): -; *Phlaeothrips* (Mickoleit 1961): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Mayer 1954): -; *Pseudomenopon* (Haub 1967): /; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): /; *Trimenopon* (Mayer 1954): -; *Bovicola* (Mayer 1954): -; *Ornithobius* (Haub 1971): /; *Columbicola* (ps): -; *Haematopinus* (Tröster 1997): -; *Hybophthirus* (Tröster 1997): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): /; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Vilhelmsen 2000): -; *Osmylus* (Beutel et al. 2010): /; *Schizodactylus* (Khattar 1964): /; *Oniscigaster* (Staniczek 2001): /; *Zorotypus* (Friedrich & Beutel 2008): ldvm2; *Perla* (Chisholm 1962): -

ldvm3, M. cervico-occipitalis posterior
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1960a): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1963): -; *Triatoma* (Barth 1952a,b, 1953a,b): /; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): /; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): /; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): /; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): /; *Aeolothrips intermedius* (Moritz 1982c): -; *Thrips* (Mickoleit 1961): -; *Haplothrips* (Mickoleit 1961): -; *Phlaeothrips* (Mickoleit 1961): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Mayer 1954): -; *Pseudomenopon* (Haub 1967): /; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): /; *Trimenopon* (Mayer 1954): -; *Bovicola* (Mayer 1954): -; *Ornithobius* (Haub 1971): /; *Columbicola* (ps): -; *Haematopinus* (Tröster 1997): -; *Hybophthirus* (Tröster 1997): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): /; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Vilhelmsen 2000): -; *Osmylus* (Beutel et al. 2010): /; *Schizodactylus* (Khattar 1964): /; *Oniscigaster* (Staniczek 2001): /; *Zorotypus* (Friedrich & Beutel 2008): ldvm3; *Perla* (Chisholm 1962): -

ldvm4, M. pronoto-cervicalis lateralis
Systelloderes (Spangenberg et al. 2013b): M3; *Cryptostemma* (Spangenberg et al. 2013b): M3; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): TM2; *Corixa* (Benwitz 1956): depr cap; *Gelastocoris* (Parsons 1960a): TM2; *Lethocerus* (Parsons 1968): 2;

Belostoma (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): cranial flexor; *Gerris* (Spangenberg et al. 2013b): M3; *Hydrometra* (Sprague 1956): M10; *Saldula* (Parsons 1963): 2; *Triatoma* (Barth 1952a,b, 1953a,b): /; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): M3; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): 43; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): +; *Psylla* (Weber 1929): Odlm1; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): +; *Pseudococcus* (ps): + (Fig. 10D); *Perissopneumon* (Singh 1971): 43; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): /; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): /; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): /; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): /; *Aeolothrips intermedius* (Moritz 1982c): M.36; *Thrips* (Mickoleit 1961): M. depr. cap. terg.; *Haplothrips* (Mickoleit 1961): M. depr. cap. terg.; *Phlaeothrips* (Mickoleit 1961): M. depr. cap. terg.; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): T; *Caecilius* (ps): +; *Cerobasis* (ps): +; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Mayer 1954): 0,l lm2; *Pseudomenopon* (Haub 1967): /; *Piagetiella* (ps): +; *Trochiloecetes* (Haub 1983): /; *Trimenopon* (Mayer 1954): 0,l lm2; *Bovicola* (Mayer 1954): 0,l lm2; *Ornithobius* (Haub 1971): /; *Columbicola* (ps): + (Fig. 22H); *Haematopinus* (Tröster 1997): M4; *Hybophthirus* (Tröster 1997): M4; *Pediculus* (ps): + (Fig. 25I); *Phthirus* (Hirsch 1986): /; *Haematomyzus* (Weber 1969): 32; *Macroxyela* (Vilhelmsen 2000): -; *Osmylus* (Beutel et al. 2010): /; *Schizodactylus* (Khattar 1964): /; *Oniscigaster* (Staniczek 2001): /; *Zorotypus* (Friedrich & Beutel 2008): ldvm4; *Perla* (Chisholm 1962): No.12

ldvm5, M. pronoto-cervicalis anterior

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1960a): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1963): -; *Triatoma* (Barth 1952a,b, 1953a,b): /; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): /; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): /; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): /; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): /; *Aeolothrips intermedius* (Moritz 1982c): -; *Thrips* (Mickoleit 1961): -; *Haplothrips* (Mickoleit 1961): -; *Phlaeothrips* (Mickoleit 1961): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Mayer 1954): -; *Pseudomenopon* (Haub 1967): /; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): /; *Trimenopon* (Mayer 1954): -; *Bovicola* (Mayer 1954): -; *Ornithobius* (Haub 1971): /; *Columbicola* (ps): -; *Haematopinus* (Tröster 1997): -; *Hybophthirus* (Tröster 1997): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): /; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Vilhelmsen 2000): 5; *Osmylus* (Beutel et al. 2010): /; *Schizodactylus* (Khattar 1964): /; *Oniscigaster* (Staniczek 2001): /; *Zorotypus* (Friedrich & Beutel 2008): -; *Perla* (Chisholm 1962): Nos.4, 5

ldvm6, M. pronoto-cervicalis medialis

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1960a): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): -; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1963): -; *Triatoma* (Barth 1952a,b, 1953a,b): /; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): -;

Hemiodoecus (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): 54; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): Oism1; *Aleurolobus* (Singh 1971): 54; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): +; *Perissopneumon* (Singh 1971): 54; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): /; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): /; *Platypleura* (Singh 1971): 54; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): /; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): /; *Aeolothrips intermedius* (Moritz 1982c): -; *Thrips* (Mickoleit 1961): -; *Haplothrips* (Mickoleit 1961): -; *Phlaeothrips* (Mickoleit 1961): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): S; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Mayer 1954): -; *Pseudomenopon* (Haub 1967): /; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): /; *Trimenopon* (Mayer 1954): -; *Bovicola* (Mayer 1954): -; *Ornithobius* (Haub 1971): /; *Columbicola* (ps): -; *Haematopinus* (Tröster 1997): -; *Hybophthirus* (Tröster 1997): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): /; *Haematomyzus* (Weber 1969): 56 + 57; *Macroxyela* (Vilhelmsen 2000): -; *Osmylus* (Beutel et al. 2010): /; *Schizodactylus* (Khattar 1964): /; *Oniscigaster* (Staniczek 2001): /; *Zorotypus* (Friedrich & Beutel 2008): Idvm6; *Perla* (Chisholm 1962): Nos.2, 3

Idvm9, M. profurca-occipitalis

Systelloderes (Spangenberg et al. 2013b): M5b; *Cryptostemma* (Spangenberg et al. 2013b): M5b; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): TM7; *Corixa* (Benwitz 1956): lev cap; *Gelastocoris* (Parsons 1960a): TM7; *Lethocerus* (Parsons 1968): 7; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): M5b; *Hydrometra* (Sprague 1956): M6; *Saldula* (Parsons 1963): 7; *Triatoma* (Barth 1952a,b, 1953a,b): /; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): Ovlm4; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): Ovlm2; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): +; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): /; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): /; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): /; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): /; *Aeolothrips intermedius* (Moritz 1982c): M.34; *Thrips* (Mickoleit 1961): -; *Haplothrips* (Mickoleit 1961): -; *Phlaeothrips* (Mickoleit 1961): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): + (Figs. 16F,G); *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Mayer 1954): -; *Pseudomenopon* (Haub 1967): /; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): /; *Trimenopon* (Mayer 1954): -; *Bovicola* (Mayer 1954): -; *Ornithobius* (Haub 1971): /; *Columbicola* (ps): -; *Haematopinus* (Tröster 1997): -; *Hybophthirus* (Tröster 1997): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): /; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Vilhelmsen 2000): 2; *Osmylus* (Beutel et al. 2010): /; *Schizodactylus* (Khattar 1964): /; *Oniscigaster* (Staniczek 2001): /; *Zorotypus* (Friedrich & Beutel 2008): -; *Perla* (Chisholm 1962): No.13

Idvmx1, "M. pronoto-tentorialis primus"

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1960a): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1963): -; *Triatoma* (Barth 1952a,b, 1953a,b): /; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): M4; *Hemiodoecus* (Singh 1971): 44; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): m. tent2; *Macrosiphum* (Singh 1971): 44; *Dactylosphaera* (Rilling 1960): 25; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): 44; *Aleyrodes* (ps): +; *Psylla* (Weber 1929): m. tent2; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): +; *Pseudococcus* (ps): + (Figs. 10E,F, 11B);

Perissopneumon (Singh 1971): 44; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): /; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): /; *Platypleura* (Singh 1971): 44; *Oxyrhachis* (Singh 1971): 44; *Scolops* (Kramer 1950): /; *Melicharia* (Singh 1971): 44; *Dictyophara* (ps): +; *Aeolothrips fasciatus* (Mickoleit 1963): /; *Aeolothrips intermedius* (Moritz 1982c): -; *Thrips* (Mickoleit 1961): -; *Haplothrips* (Mickoleit 1961): -; *Phlaeothrips* (Mickoleit 1961): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Mayer 1954): -; *Pseudomenopon* (Haub 1967): /; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): /; *Trimenopon* (Mayer 1954): -; *Bovicola* (Mayer 1954): -; *Ornithobius* (Haub 1971): /; *Columbicola* (ps): -; *Haematopinus* (Tröster 1997): -; *Hybophthirus* (Tröster 1997): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): /; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Vilhelmsen 2000): -; *Osmylus* (Beutel et al. 2010): /; *Schizodactylus* (Khattar 1964): /; *Oniscigaster* (Staniczek 2001): /; *Zorotypus* (Friedrich & Beutel 2008): -; *Perla* (Chisholm 1962): -

ldvmx2, "M. pronoto-genalis"

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1960a): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1963): -; *Triatoma* (Barth 1952a,b, 1953a,b): /; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): 49; *Cacopsylla* (ps): +; *Pseudococcus* (ps): + (Figs. 10G, 11B,C); *Perissopneumon* (Singh 1971): 49; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): /; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): /; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): /; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): /; *Aeolothrips intermedius* (Moritz 1982c): -; *Thrips* (Mickoleit 1961): -; *Haplothrips* (Mickoleit 1961): -; *Phlaeothrips* (Mickoleit 1961): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Mayer 1954): -; *Pseudomenopon* (Haub 1967): /; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): /; *Trimenopon* (Mayer 1954): -; *Bovicola* (Mayer 1954): -; *Ornithobius* (Haub 1971): /; *Columbicola* (ps): -; *Haematopinus* (Tröster 1997): -; *Hybophthirus* (Tröster 1997): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): /; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Vilhelmsen 2000): -; *Osmylus* (Beutel et al. 2010): /; *Schizodactylus* (Khattar 1964): /; *Oniscigaster* (Staniczek 2001): /; *Zorotypus* (Friedrich & Beutel 2008): -; *Perla* (Chisholm 1962): -

ldvmx3, "M. proepisterno-occipitalis"

Systelloderes (Spangenberg et al. 2013b): M2a; *Cryptostemma* (Spangenberg et al. 2013b): M2a; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): TM10a; *Corixa* (Benwitz 1956): rot cap2; *Gelastocoris* (Parsons 1960a): TM10a; *Lethocerus* (Parsons 1968): 6a; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): M2a; *Hydrometra* (Sprague 1956): M7; *Saldula* (Parsons 1963): -; *Triatoma* (Barth 1952a,b, 1953a,b): /; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): 52; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): Ovlm2; *Macrosiphum* (Singh 1971): 52; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): 52; *Aleyrodes* (ps): +; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): 52; *Cacopsylla* (ps): +; *Pseudococcus* (ps): + (Fig. 10G); *Perissopneumon* (Singh 1971): 52; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): /; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): /; *Platypleura* (Singh 1971): 52; *Oxyrhachis* (Singh 1971): 52; *Scolops* (Kramer 1950): /; *Melicharia* (Singh 1971): 52; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): /; *Aeolothrips intermedius* (Moritz 1982c): -; *Thrips* (Mickoleit 1961): -;

Haplothrips (Mickoleit 1961): -; *Phlaeothrips* (Mickoleit 1961): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Mayer 1954): -; *Pseudomenopon* (Haub 1967): /; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): /; *Trimenopon* (Mayer 1954): -; *Bovicola* (Mayer 1954): -; *Ornithobius* (Haub 1971): /; *Columbicola* (ps): -; *Haematopinus* (Tröster 1997): -; *Hybophthirus* (Tröster 1997): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): /; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Vilhelmsen 2000): -; *Osmylus* (Beutel et al. 2010): /; *Schizodactylus* (Khattar 1964): /; *Oniscigaster* (Staniczek 2001): /; *Zorotypus* (Friedrich & Beutel 2008): -; *Perla* (Chisholm 1962): -

ldvmx4, "M. pronoto-tentorialis secundus"

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1960a): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1963): -; *Triatoma* (Barth 1952a,b, 1953a,b): /; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): 45; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): m. tent1; *Macrosiphum* (Singh 1971): 45; *Dactylosphaera* (Rilling 1960): 23 + 24; *Trialeurodes* (Weber 1935): m. tentorii; *Aleurolobus* (Singh 1971): 45; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): m. tent1; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): +; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): /; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): /; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): /; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): /; *Aeolothrips intermedius* (Moritz 1982c): -; *Thrips* (Mickoleit 1961): -; *Haplothrips* (Mickoleit 1961): -; *Phlaeothrips* (Mickoleit 1961): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Mayer 1954): -; *Pseudomenopon* (Haub 1967): /; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): /; *Trimenopon* (Mayer 1954): -; *Bovicola* (Mayer 1954): -; *Ornithobius* (Haub 1971): /; *Columbicola* (ps): -; *Haematopinus* (Tröster 1997): -; *Hybophthirus* (Tröster 1997): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): /; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Vilhelmsen 2000): -; *Osmylus* (Beutel et al. 2010): /; *Schizodactylus* (Khattar 1964): /; *Oniscigaster* (Staniczek 2001): /; *Zorotypus* (Friedrich & Beutel 2008): -; *Perla* (Chisholm 1962): -

ldvmx5, "M. sterno-cervicalis"

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1960a): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1963): -; *Triatoma* (Barth 1952a,b, 1953a,b): /; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): /; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): /; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): /; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): /; *Aeolothrips intermedius* (Moritz 1982c): -; *Thrips* (Mickoleit 1961): -; *Haplothrips* (Mickoleit 1961): -; *Phlaeothrips* (Mickoleit 1961): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Mayer 1954): -; *Pseudomenopon* (Haub 1967): /; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): /; *Trimenopon* (Mayer 1954): -; *Bovicola* (Mayer 1954): -; *Ornitho-*

bius (Haub 1971): /; *Columbicola* (ps): -; *Haematopinus* (Tröster 1997): -; *Hybophthirus* (Tröster 1997): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): /; *Haematomyzus* (Weber 1969): 41 + 42 + 63; *Macroxyela* (Vilhelmsen 2000): -; *Osmylus* (Beutel et al. 2010): /; *Schizodactylus* (Khattar 1964): /; *Oniscigaster* (Staniczek 2001): /; *Zorotypus* (Friedrich & Beutel 2008): -; *Perla* (Chisholm 1962): -

Tergo-pleural extrinsic head muscles

ltpm1, M. pleurocrista-occipitalis
Systelloderes (Spangenberg et al. 2013b): M1; *Cryptostemma* (Spangenberg et al. 2013b): M1; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): TM10b; *Corixa* (Benwitz 1956): rot cap1; *Gelastocoris* (Parsons 1960a): TM10b; *Lethocerus* (Parsons 1968): 10; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): M1; *Hydrometra* (Sprague 1956): M1; *Saldula* (Parsons 1963): 10; *Triatoma* (Barth 1952a,b, 1953a,b): /; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): M1; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): Odvm; *Macrosiphum* (Singh 1971): 50; *Dactylosphaera* (Rilling 1960): 54; *Trialeurodes* (Weber 1935): Odvm; *Aleurolobus* (Singh 1971): 50; *Aleyrodes* (ps): +; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): 50; *Cacopsylla* (ps): +; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): /; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): /; *Platypleura* (Singh 1971): 50; *Oxyrhachis* (Singh 1971): 50; *Scolops* (Kramer 1950): /; *Melicharia* (Singh 1971): 50; *Dictyophara* (ps): +; *Aeolothrips fasciatus* (Mickoleit 1963): /; *Aeolothrips intermedius* (Moritz 1982c): -; *Thrips* (Mickoleit 1961): -; *Haplothrips* (Mickoleit 1961): -; *Phlaeothrips* (Mickoleit 1961): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): LL; *Caecilius* (ps): +; *Cerobasis* (ps): + (Figs. 16F,G,H); *Troctes* (Noland 1924): /; *Liposcelis* (ps): +; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Mayer 1954): 0,l lm1; *Pseudomenopon* (Haub 1967): /; *Piagetiella* (ps): +; *Trochiloecetes* (Haub 1983): /; *Trimenopon* (Mayer 1954): 0,l lm1; *Bovicola* (Mayer 1954): 0,l lm1; *Ornithobius* (Haub 1971): /; *Columbicola* (ps): + (Fig. 22H); *Haematopinus* (Tröster 1997): M3; *Hybophthirus* (Tröster 1997): M3; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): /; *Haematomyzus* (Weber 1969): 29-31 + 33; *Macroxyela* (Vilhelmsen 2000): 1; *Osmylus* (Beutel et al. 2010): /; *Schizodactylus* (Khattar 1964): /; *Oniscigaster* (Staniczek 2001): /; *Zorotypus* (Friedrich & Beutel 2008): ltpm1; *Perla* (Chisholm 1962): No.1

ltpm2, M. propleuro-occipitalis
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1960a): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1963): -; *Triatoma* (Barth 1952a,b, 1953a,b): /; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): /; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): /; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): /; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): /; *Aeolothrips intermedius* (Moritz 1982c): -; *Thrips* (Mickoleit 1961): -; *Haplothrips* (Mickoleit 1961): -; *Phlaeothrips* (Mickoleit 1961): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Mayer 1954): -; *Pseudomenopon* (Haub 1967): /; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): /; *Trimenopon* (Mayer 1954): -; *Bovicola* (Mayer 1954): -; *Ornithobius* (Haub 1971): /; *Columbicola* (ps): -; *Haematopinus* (Tröster 1997): -; *Hybophthirus* (Tröster 1997): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): /; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Vilhel-

msen 2000): -; *Osmylus* (Beutel et al. 2010): /; *Schizodactylus* (Khattar 1964): /; *Oniscigaster* (Staniczek 2001): /; *Zorotypus* (Friedrich & Beutel 2008): ltpm2; *Perla* (Chisholm 1962): -

Pleuro-coxal extrinsic head muscles

lpcm1, M. procoxa-cervicalis
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1960a): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1963): -; *Triatoma* (Barth 1952a,b, 1953a,b): /; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): /; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): /; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): /; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): /; *Aeolothrips intermedius* (Moritz 1982c): M.32; *Thrips* (Mickoleit 1961): M. cerv.-postocc. (Although the name suggests that this muscle originates from the cervical sclerite, Mickoleit [1961] showed that the origin is shifted to the trochanter.); *Haplothrips* (Mickoleit 1961): M. cerv.-postocc.; *Phlaeothrips* (Mickoleit 1961): M. cerv.-postocc.; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): DVL (the origin of this muscle is shifted from the cervical sclerite to the trochantinus according to Mickoleit [1961]. This assumption is supported by the condition in *Stenopsocus*, where one portion originates from the trochantinus [DVL2] whereas the other is shifted to the cervical sclerite [DVL1] [Badonnel 1934]. Friedrich & Beutel [2008] homologized DVL1 with Idlm2. However, the later originates on the pronotum whereas it is the sternal region and the lateral cervical sclerite in the former.); *Caecilius* (ps): +; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Mayer 1954): -; *Pseudomenopon* (Haub 1967): /; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): /; *Trimenopon* (Mayer 1954): -; *Bovicola* (Mayer 1954): -; *Ornithobius* (Haub 1971): /; *Columbicola* (ps): -; *Haematopinus* (Tröster 1997): -; *Hybophthirus* (Tröster 1997): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): /; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Vilhelmsen 2000): -; *Osmylus* (Beutel et al. 2010): /; *Schizodactylus* (Khattar 1964): /; *Oniscigaster* (Staniczek 2001): /; *Zorotypus* (Friedrich & Beutel 2008): -; *Perla* (Chisholm 1962): -

lpcm2, M. procoxa-cervicalis transversalis
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1960a): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1963): -; *Triatoma* (Barth 1952a,b, 1953a,b): /; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): /; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): /; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): /; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): /; *Aeolothrips intermedius* (Moritz 1982c): -; *Thrips* (Mickoleit 1961): -; *Haplothrips* (Mickoleit 1961): -; *Phlaeothrips* (Mickoleit 1961): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): X1; *Caecilius* (ps): +; *Cerobasis* (ps): + (Fig. 16H); *Troctes*

(Noland 1924): /; *Liposcelis* (ps): +; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Mayer 1954): O, I trm; *Pseudomenopon* (Haub 1967): /; *Piagetiella* (ps): +; *Trochiloecetes* (Haub 1983): /; *Trimenopon* (Mayer 1954): -; *Bovicola* (Mayer 1954): -; *Ornithobius* (Haub 1971): /; *Columbicola* (ps): -; *Haematopinus* (Tröster 1997): -; *Hybophthirus* (Tröster 1997): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): /; *Haematomyzus* (Weber 1969): 44; *Macroxyela* (Vilhelmsen 2000): 7; *Osmylus* (Beutel et al. 2010): /; *Schizodactylus* (Khattar 1964): /; *Oniscigaster* (Staniczek 2001): /; *Zorotypus* (Friedrich & Beutel 2008): -; *Perla* (Chisholm 1962): Nos. 21, 22

lpcmx1, "M. coxa-cervicalis secundus"
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1960a): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1963): -; *Triatoma* (Barth 1952a,b, 1953a,b): /; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): /; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): /; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): /; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): /; *Aeolothrips intermedius* (Moritz 1982c): -; *Thrips* (Mickoleit 1961): -; *Haplothrips* (Mickoleit 1961): -; *Phlaeothrips* (Mickoleit 1961): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Mayer 1954): -; *Pseudomenopon* (Haub 1967): /; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): /; *Trimenopon* (Mayer 1954): -; *Bovicola* (Mayer 1954): -; *Ornithobius* (Haub 1971): /; *Columbicola* (ps): -; *Haematopinus* (Tröster 1997): -; *Hybophthirus* (Tröster 1997): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): /; *Haematomyzus* (Weber 1969): 45; *Macroxyela* (Vilhelmsen 2000): -; *Osmylus* (Beutel et al. 2010): /; *Schizodactylus* (Khattar 1964): /; *Oniscigaster* (Staniczek 2001): /; *Zorotypus* (Friedrich & Beutel 2008): -; *Perla* (Chisholm 1962): -

lpcmx2, "M. coxa-cervicalis tertius"
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1960a): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1963): -; *Triatoma* (Barth 1952a,b, 1953a,b): /; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): /; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): /; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): /; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): /; *Aeolothrips intermedius* (Moritz 1982c): -; *Thrips* (Mickoleit 1961): -; *Haplothrips* (Mickoleit 1961): -; *Phlaeothrips* (Mickoleit 1961): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Mayer 1954): -; *Pseudomenopon* (Haub 1967): /; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): /; *Trimenopon* (Mayer 1954): -; *Bovicola* (Mayer 1954): -; *Ornithobius* (Haub 1971): /; *Columbicola* (ps): -; *Haematopinus* (Tröster 1997): -; *Hybophthirus* (Tröster 1997): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): /; *Haematomyzus*

(Weber 1969): 50; *Macroxyela* (Vilhelmsen 2000): -; *Osmylus* (Beutel et al. 2010): /; *Schizodactylus* (Khattar 1964): /; *Oniscigaster* (Staniczek 2001): /; *Zorotypus* (Friedrich & Beutel 2008): -; *Perla* (Chisholm 1962): -

lpcmx3, "M. coxa-cervicalis quartus"
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1960a): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1963): -; *Triatoma* (Barth 1952a,b, 1953a,b): /; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): /; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): /; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): /; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): /; *Aeolothrips intermedius* (Moritz 1982c): -; *Thrips* (Mickoleit 1961): -; *Haplothrips* (Mickoleit 1961): -; *Phlaeothrips* (Mickoleit 1961): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Mayer 1954): -; *Pseudomenopon* (Haub 1967): /; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): /; *Trimenopon* (Mayer 1954): -; *Bovicola* (Mayer 1954): -; *Ornithobius* (Haub 1971): /; *Columbicola* (ps): -; *Haematopinus* (Tröster 1997): -; *Hybophthirus* (Tröster 1997): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): /; *Haematomyzus* (Weber 1969): 51; *Macroxyela* (Vilhelmsen 2000): -; *Osmylus* (Beutel et al. 2010): /; *Schizodactylus* (Khattar 1964): /; *Oniscigaster* (Staniczek 2001): /; *Zorotypus* (Friedrich & Beutel 2008): -; *Perla* (Chisholm 1962): -

lpcmx4, "M. coxa-cervicalis quintus"
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1960a): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1963): -; *Triatoma* (Barth 1952a,b, 1953a,b): /; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): /; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): /; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): /; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): /; *Aeolothrips intermedius* (Moritz 1982c): -; *Thrips* (Mickoleit 1961): -; *Haplothrips* (Mickoleit 1961): -; *Phlaeothrips* (Mickoleit 1961): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Mayer 1954): -; *Pseudomenopon* (Haub 1967): /; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): /; *Trimenopon* (Mayer 1954): -; *Bovicola* (Mayer 1954): -; *Ornithobius* (Haub 1971): /; *Columbicola* (ps): -; *Haematopinus* (Tröster 1997): -; *Hybophthirus* (Tröster 1997): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): /; *Haematomyzus* (Weber 1969): 38; *Macroxyela* (Vilhelmsen 2000): -; *Osmylus* (Beutel et al. 2010): /; *Schizodactylus* (Khattar 1964): /; *Oniscigaster* (Staniczek 2001): /; *Zorotypus* (Friedrich & Beutel 2008): -; *Perla* (Chisholm 1962): -

Ventral longitudinal extrinsic head muscles

lvlm1, M. profurca-cervicalis
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1960a): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1963): -; *Triatoma* (Barth 1952a,b, 1953a,b): /; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): /; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): /; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): /; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): /; *Aeolothrips intermedius* (Moritz 1982c): -; *Thrips* (Mickoleit 1961): -; *Haplothrips* (Mickoleit 1961): -; *Phlaeothrips* (Mickoleit 1961): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): +; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Mayer 1954): -; *Pseudomenopon* (Haub 1967): /; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): /; *Trimenopon* (Mayer 1954): -; *Bovicola* (Mayer 1954): -; *Ornithobius* (Haub 1971): /; *Columbicola* (ps): -; *Haematopinus* (Tröster 1997): -; *Hybophthirus* (Tröster 1997): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): /; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Vilhelmsen 2000): 6; *Osmylus* (Beutel et al. 2010): /; *Schizodactylus* (Khattar 1964): /; *Oniscigaster* (Staniczek 2001): /; *Zorotypus* (Friedrich & Beutel 2008): -; *Perla* (Chisholm 1962): -

lvlm2, M. submento-cervicalis
Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1960a): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1963): -; *Triatoma* (Barth 1952a,b, 1953a,b): /; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): /; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): /; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): /; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): /; *Aeolothrips intermedius* (Moritz 1982c): -; *Thrips* (Mickoleit 1961): -; *Haplothrips* (Mickoleit 1961): -; *Phlaeothrips* (Mickoleit 1961): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Mayer 1954): -; *Pseudomenopon* (Haub 1967): /; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): /; *Trimenopon* (Mayer 1954): -; *Bovicola* (Mayer 1954): -; *Ornithobius* (Haub 1971): /; *Columbicola* (ps): -; *Haematopinus* (Tröster 1997): -; *Hybophthirus* (Tröster 1997): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): /; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Vilhelmsen 2000): -; *Osmylus* (Beutel et al. 2010): /; *Schizodactylus* (Khattar 1964): /; *Oniscigaster* (Staniczek 2001): /; *Zorotypus* (Friedrich & Beutel 2008): -; *Perla* (Chisholm 1962): No.14

lvlm3, M. profurca-tentorialis

Systelloderes (Spangenberg et al. 2013b): M5; *Cryptostemma* (Spangenberg et al. 2013b): M5; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): TM6; *Corixa* (Benwitz 1956): retr cap3; *Gelastocoris* (Parsons 1960a): TM6; *Lethocerus* (Parsons 1968): 6B; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): M5; *Hydrometra* (Sprague 1956): M6; *Saldula* (Parsons 1963): 6; *Triatoma* (Barth 1952a,b, 1953a,b): /; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): M5; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): Ovlm4; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): 37; *Trialeurodes* (Weber 1935): Ovlm; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): +; *Psylla* (Weber 1929): Ovlm3; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): +; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): /; *Philaenus* (ps): +; *Lepyronia* (Kramer 1950): /; *Platypleura* (Singh 1971): 51; *Oxyrhachis* (Singh 1971): 51; *Scolops* (Kramer 1950): /; *Melicharia* (Singh 1971): 51; *Dictyophara* (ps): +; *Aeolothrips fasciatus* (Mickoleit 1963): /; *Aeolothrips intermedius* (Moritz 1982c): M.35; *Thrips* (Mickoleit 1961): M. depr. cap. furc. lat.; *Haplothrips* (Mickoleit 1961): M. depr. cap. furc. lat.; *Phlaeothrips* (Mickoleit 1961): M. depr. cap. furc. lat.; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): LV1; *Caecilius* (ps): +; *Cerobasis* (ps): + (Fig. 16H); *Troctes* (Noland 1924): /; *Liposcelis* (ps): + (Fig. 18J); *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Mayer 1954): 0,I vlm; *Pseudomenopon* (Haub 1967): /; *Piagetiella* (ps): + (Figs. 20G,H); *Trochiloecetes* (Haub 1983): /; *Trimenopon* (Mayer 1954): 0,I vlm1; *Bovicola* (Mayer 1954): -; *Ornithobius* (Haub 1971): /; *Columbicola* (ps): -; *Haematopinus* (Tröster 1997): -; *Hybophthirus* (Tröster 1997): -; *Pediculus* (ps): +; *Phthirus* (Hirsch 1986): /; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Vilhelmsen 2000): 3; *Osmylus* (Beutel et al. 2010): /; *Schizodactylus* (Khattar 1964): /; *Oniscigaster* (Staniczek 2001): /; *Zorotypus* (Friedrich & Beutel 2008): lvlm3; *Perla* (Chisholm 1962): No.18

lvlmx1

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1960a): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1963): -; *Triatoma* (Barth 1952a,b, 1953a,b): /; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): Ovlm1; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): Ovlm1; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): ? (53); *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): /; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): /; *Platypleura* (Singh 1971): ? (53); *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): /; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): /; *Aeolothrips intermedius* (Moritz 1982c): -; *Thrips* (Mickoleit 1961): -; *Haplothrips* (Mickoleit 1961): -; *Phlaeothrips* (Mickoleit 1961): -.; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Mayer 1954): -; *Pseudomenopon* (Haub 1967): /; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): /; *Trimenopon* (Mayer 1954): -; *Bovicola* (Mayer 1954): -; *Ornithobius* (Haub 1971): /; *Columbicola* (ps): -; *Haematopinus* (Tröster 1997): -; *Hybophthirus* (Tröster 1997): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): /; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Vilhelmsen 2000): -; *Osmylus* (Beutel et al. 2010): /; *Schizodactylus* (Khattar 1964): /; *Oniscigaster* (Staniczek 2001): /; *Zorotypus* (Friedrich & Beutel 2008): -; *Perla* (Chisholm 1962): -

lvlmx2

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1960a): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1963): -; *Triatoma* (Barth 1952a,b, 1953a,b): /; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): /; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): /; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): /; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): /; *Aeolothrips intermedius* (Moritz 1982c): -; *Thrips* (Mickoleit 1961): -; *Haplothrips* (Mickoleit 1961): -; *Phlaeothrips* (Mickoleit 1961): -.; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Mayer 1954): -; *Pseudomenopon* (Haub 1967): /; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): /; *Trimenopon* (Mayer 1954): -; *Bovicola* (Mayer 1954): -; *Ornithobius* (Haub 1971): /; *Columbicola* (ps): -; *Haematopinus* (Tröster 1997): -; *Hybophthirus* (Tröster 1997): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): /; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Vilhelmsen 2000): -; *Osmylus* (Beutel et al. 2010): /; *Schizodactylus* (Khattar 1964): /; *Oniscigaster* (Staniczek 2001): /; *Zorotypus* (Friedrich & Beutel 2008): -; *Perla* (Chisholm 1962): No.19

Dorsal transverse extrinsic head muscles

ldx1, "M. cervico-cervicalis"

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1960a): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1963): -; *Triatoma* (Barth 1952a,b, 1953a,b): /; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): /; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): /; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): /; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): /; *Aeolothrips intermedius* (Moritz 1982c): -; *Thrips* (Mickoleit 1961): -; *Haplothrips* (Mickoleit 1961): -; *Phlaeothrips* (Mickoleit 1961): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Mayer 1954): -; *Pseudomenopon* (Haub 1967): /; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): /; *Trimenopon* (Mayer 1954): -; *Bovicola* (Mayer 1954): -; *Ornithobius* (Haub 1971): /; *Columbicola* (ps): -; *Haematopinus* (Tröster 1997): -; *Hybophthirus* (Tröster 1997): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): /; *Haematomyzus* (Weber 1969): 43; *Macroxyela* (Vilhelmsen 2000): -; *Osmylus* (Beutel et al. 2010): /; *Schizodactylus* (Khattar 1964): /; *Oniscigaster* (Staniczek 2001): /; *Zorotypus* (Friedrich & Beutel 2008): -; *Perla* (Chisholm 1962): -

Idx2, "Mxy"

Systelloderes (Spangenberg et al. 2013b): -; *Cryptostemma* (Spangenberg et al. 2013b): -; *Hypsipteryx* (Štys 1970): /; Schizopteridae (Emsley 1969): /; *Ochterus* (Rieger 1976): -; *Corixa* (Benwitz 1956): -; *Gelastocoris* (Parsons 1960a): -; *Lethocerus* (Parsons 1968): -; *Belostoma* (Verma et al. 1973): /; *Hydrocyrius* (Kopelke 1978): /; *Nepa* (Hamilton 1931, Rieger 1976): /; *Gerris* (Spangenberg et al. 2013b): -; *Hydrometra* (Sprague 1956): -; *Saldula* (Parsons 1963): -; *Triatoma* (Barth 1952a,b, 1953a,b): /; *Dysdercus* (Khan 1972): /; *Hackeriella* (Spangenberg et al. 2013a): -; *Hemiodoecus* (Singh 1971): -; *Pantinia* (Spangenberg et al. 2013a): /; *Peloridium* (Spangenberg et al. 2013a): /; *Aphis* (Weber 1928): -; *Macrosiphum* (Singh 1971): -; *Dactylosphaera* (Rilling 1960): -; *Trialeurodes* (Weber 1935): -; *Aleurolobus* (Singh 1971): -; *Aleyrodes* (ps): -; *Psylla* (Weber 1929): -; *Diaphorina* (Singh 1971): -; *Cacopsylla* (ps): -; *Pseudococcus* (ps): -; *Perissopneumon* (Singh 1971): -; *Tibicina* (Snodgrass 1927; Kramer 1950): /; *Idiocerus* (Arora & Singh 1962): /; *Philaenus* (ps): -; *Lepyronia* (Kramer 1950): /; *Platypleura* (Singh 1971): -; *Oxyrhachis* (Singh 1971): -; *Scolops* (Kramer 1950): /; *Melicharia* (Singh 1971): -; *Dictyophara* (ps): -; *Aeolothrips fasciatus* (Mickoleit 1963): /; *Aeolothrips intermedius* (Moritz 1982c): -; *Thrips* (Mickoleit 1961): -; *Haplothrips* (Mickoleit 1961): -; *Phlaeothrips* (Mickoleit 1961): -; *Psocus* (Cope 1940): /; *Psococerastis* (Masumoto & Nagashima 1993): /; *Stenopsocus* (Badonnel 1934): -; *Caecilius* (ps): -; *Cerobasis* (ps): -; *Troctes* (Noland 1924): /; *Liposcelis* (ps): -; *Gliricola* (Risler & Geising 1965): /; *Myrsidea* (Mayer 1954): -; *Pseudomenopon* (Haub 1967): /; *Piagetiella* (ps): -; *Trochiloecetes* (Haub 1983): /; *Trimenopon* (Mayer 1954): -; *Bovicola* (Mayer 1954): -; *Ornithobius* (Haub 1971): /; *Columbicola* (ps): -; *Haematopinus* (Tröster 1997): -; *Hybophthirus* (Tröster 1997): -; *Pediculus* (ps): -; *Phthirus* (Hirsch 1986): /; *Haematomyzus* (Weber 1969): -; *Macroxyela* (Vilhelmsen 2000): -; *Osmylus* (Beutel et al. 2010): /; *Schizodactylus* (Khattar 1964): /; *Oniscigaster* (Staniczek 2001): /; *Zorotypus* (Friedrich & Beutel 2008): Mxy; *Perla* (Chisholm 1962): -

8.2 Appendix 2: Phylogeny resulting from the initial taxon-sampling

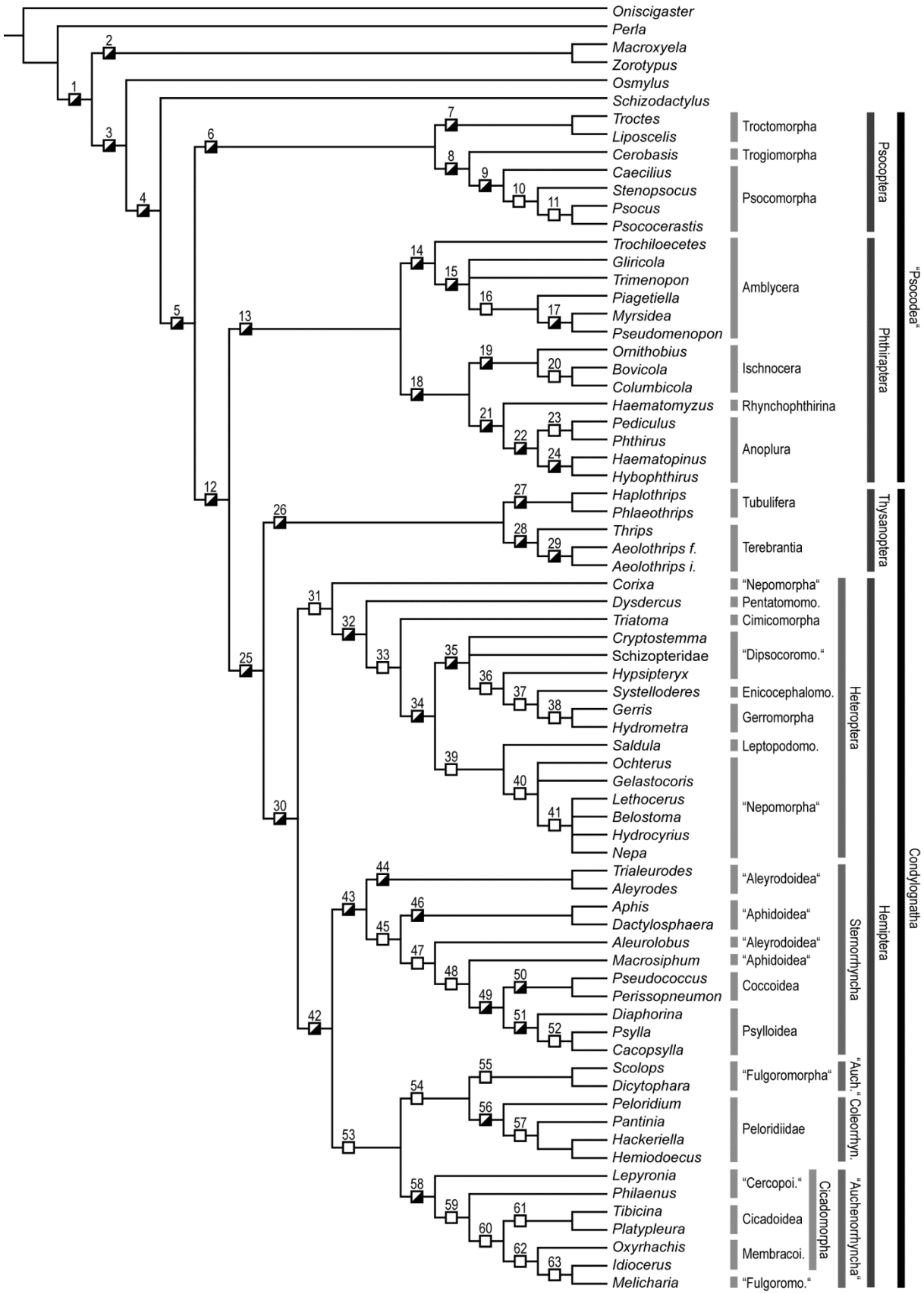

Figure A1 (previous page). Original strict consensus cladogram of 397 characters and 72 taxa (1381 steps, Ci: 34, Ri: 75, unambiguous only) calculated with WinClada. Black-and-white boxes indicate homoplasious and non-homoplasious apomorphy-complexes, white boxes only non-homoplasious ones (apomorphies of single species not labeled). Homoplasious characters are set in *italics* (not identical with those in Figs. 28 and A2). **apomorphy-complex 1**: (265/0), (370/0), (423/0), (424/0), (431/0), *(494/1)*. **2**: (9/3), *(46/0)*, *(47/0)*, *(336/1)*, *(384/1)*, *(436/1)*, *(500/0)*, *(510/1)*. **3**: *(54/1)*, (430/0), (474/0), *(490/1)*. **4**: (13/0), *(18/0)*, *(154/0)*, *(155/0)*, *(198/1)*, (432/1), *(435/0)*, *(492/1)*. **5**: *(172/1)*, (214/1), (215/1), *(218/0)*, (220/1), (230/0), (255/2), (261/0), (264/0), (272/0), *(277/0)*, *(302/1)*, *(309/0)*, (318/2), *(341/0)*, *(384/1)*, *(453/0)*, (473/0), (491/0). **6**: *(35/3)*, *(48/1)*, (143/1), *(153/1)*, (217/2), *(273/1)*, *(397/1)*, *(404/1)*, *(407/1)*, *(420/1)*, *(421/1)*. **7**: *(5/1)*, (24/0), *(109/1)*, *(388/1)*, *(483/0)*, *(515/1)*. **8**: *(37/1)*, *(155/4)*, *(247/0)*, *(263/0)*, *(303/1)*, (396/1), *(423/1)*, *(424/1)*, *(436/1)*. **9**: *(73/1)*, *(88/1)*, (144/1), *(217/1)*, *(269/0)*, (307/1), *(473/2)*. **10:** *(18/1)*, *(109/1)*, *(186/0)*. **11:** *(32/1)*, *(123/1)*. **12:** *(89/0)*, (199/1), (274/0), *(276/0)*, (326/1), *(340/0)*, *(490/0)*. **13:** *(5/1)*, (24/2), (*34/0*), *(41/1)*, *(288/0)*, *(388/1)*, *(437/0)*, *(483/0)*, *(495/1)*, *(515/1)*. **14:** *(119/1)*, *(126/1)*, (128/1), *(153/1)*, (235/1), (279/1), *(407/1)*, *(453/1)*. **15:** *(109/1)*, (271/2), *(404/1)*, *(422/1)*, *(456/0)*, *(484/0)*, *(490/1)*. **16:** *(89/1)*, *(118/1)*. **17:** *(201/1)*, *(385/1)*, (428/1), *(435/1)*, *(443/1)*, *(453/0)*, *(491/1)*. **18:** *(33/1)*, *(70/0)*, *(96/0)*, (234/0), *(247/0)*, *(254/0)*, *(270/0)*. **19:** *(50/1)*, *(58/1)*, (64/1), *(109/1)*, *(118/1)*, (122/1), *(423/1)*, *(424/1)*, *(443/1)*, *(496/1)*. **20:** *(404/1)*, *(407/1)*, *(421/1)*, *(522/1)*. **21:** *(24/3)*, *(32/1)*, *(44/0)*, *(46/1)*, *(105/0)*, *(112/0)*, (149/1), *(155/1)*, (166/1), *(172/0)*, (268/0), *(301/0)*, *(312/0)*, (369/1), (476/1). **22:** *(33/0)*, (66/1), (67/1), *(160/1)*, (168/3), (171/3), (179/1), *(183/0)*, (289/1), (313/1), (314/1), (316/1), *(317/0)*, (410/1), (411/1), (413/1), (415/1), *(436/1)*, (458/1), *(484/0)*, *(522/1)*. **23:** *(48/1)*, *(440/0)*, *(454/0)*, *(493/0)*. **24:** *(58/1)*, (102/1), (103/1), *(118/1)*, (252/1), (402/1), *(404/1)*, *(407/1)*, *(429/1)*. **25:** *(18/1)*, *(31/0)*, *(47/0)*, (59/0), (168/1), (171/1), (193/1), *(198/0)*, (221/1), *(242/0)*, (256/1), *(266/0)*, *(269/0)*, *(332/0)*, (368/1), (382/1), (387/1), (392/1), *(394/0)*, *(398/0)*, (409/1), (419/1), *(427/0)*, (468/1), *(474/1)*, *(484/0)*,*(505/1)*. **26:** (4/1), *(37/1)*, *(86/0)*, *(88/1)*, (106/1), (167/1), *(178/0)*, (236/1), *(263/3)*, *(280/1)*, *(283/1)*, (371/1), (372/1), (383/1), (390/1), (470/1), (482/1), *(486/0)*, *(493/0)*, *(517/1)*. **27:** *(54/0)*, (57/1), (176/1), *(203/1)*, (374/1), *(381/1)*, (433/1), *(485/0)*, *(500/2)*, *(510/1)*. **28:** *(36/1)*, (129/1), (161/1), *(330/1)*, *(436/1)*. **29:** *(32/1)*, *(230/1)*, *(264/1)*, *(272/1)*, (282/1), (318/0), *(336/1)*, *(488/0)*. **30:** *(10/0)*, *(19/1)*, (42/1), *(160/1)*, (162/0), (170/0), (175/1), (182/1), (189/1), *(254/0)*, *(270/0)*, (291/1), *(312/0)*, *(317/0)*, *(339/0)*, *(367/0)*, *(373/0)*, *(375/0)*, *(378/0)*, (389/0), (391/0), *(432/0)*, *(492/0)*, *(498/0)*, *(504/0)*. **31:** *(41/1)*, *(44/0)*, *(79/1)*, *(105/0)*, *(126/1)*, *(155/1)*, *(201/0)*, *(288/0)*, *(502/1)*. **32:** *(40/1)*, *(137/1)*, (139/1), *(204/1)*, *(388/1)*, *(483/0)*, *(517/1)*. **33:** *(48/1)*, *(207/1)*. **34:** (190/1), *(292/2)*, *(342/1)*. **35:** *(18/0)*, (138/2), *(493/0)*, *(502/0)*. **36:** *(40/0)*, *(56/1)*. **37:** *(138/1)*, *(298/1)*. **38:** *(60/1)*, *(218/1)*, *(256/0)*, *(502/1)*. **39:** *(33/1)*, *(47/1)*, *(300/1)*, *(471/1)*, *(490/1)*. **40:** *(119/1)*, *(120/1)*, *(139/0)*, *(218/1)*, *(293/1)*, *(298/1)*. **41:** *(18/0)*, *(190/2)*, *(207/0)*, *(256/0)*, *(518/1)*. **42:** *(76/0)*, (80/1), *(263/0)*, *(507/1)*. **43:** *(109/1)*, *(154/1)*, *(178/0)*, *(181/0)*, *(206/0)*, (259/0), *(493/0)*, *(505/0)*. **44:** *(23/1)*, *(63/0)*, (284/1), *(342/1)*, *(356/1*). **45:** *(263/1)*, *(357/1)*, *(506/0)*. **46:** *(153/1)*, *(226/1)*, (348/1), (350/1), *(353/1)*, (447/1), (449/1), *(490/1)*. **47:** *(78/1)*, *(96/0)*, *(158/1)*, *(159/1)*, *(259/1)*, *(283/1)*, *(295/1)*. **48:** *(76/1)*, *(343/0)*, *(362/1)*. **49:** (81/1), (187/2), (324/1), *(352/0)*, (354/1). **50:** (7/1), *(18/0)*, *(24/3)*, *(86/0)*, *(206/1)*, *(257/0)*, *(258/0)*, *(353/1)*, (355/1). **51:** (28/1), (30/2), *(47/1)*, *(78/0)*, *(189/0)*, *(208/0)*, (290/1). **52:** *(45/0)*, *(56/0)*, *(79/1)*, *(96/1)*, *(226/1)*, *(283/0)*, *(292/1)*, *(295/0)*, *(345/0)*, *(351/0)*, *(441/2)*, *(446/1)*, *(490/1)*. **53:** *(344/0)*, *(521/0)*. **54:** *(48/1)*, *(120/1)*, *(258/0)*. **55:** *(44/0)*, *(125/1)*, *(201/0)*. **56:** (2/1), (6/1), (8/1), (30/1), *(119/1)*. **57:** *(18/0)*. **58:** (121/1), (155/2), *(181/1)*, *(280/1)*. **59:** *(37/1)*, *(63/0)*, *(204/1)*, *(490/1)*, *(494/1)*, *(495/1)*. **60:** *(48/1)*, *(158/1)*, *(159/1)*. **61:** *(10/1)*, *(19/0)*, *(47/1)*. **62:** *(32/1)*, *(259/1)*, *(280/0)*. **63:** *(63/1)*, *(295/1)*, *(378/1)*.

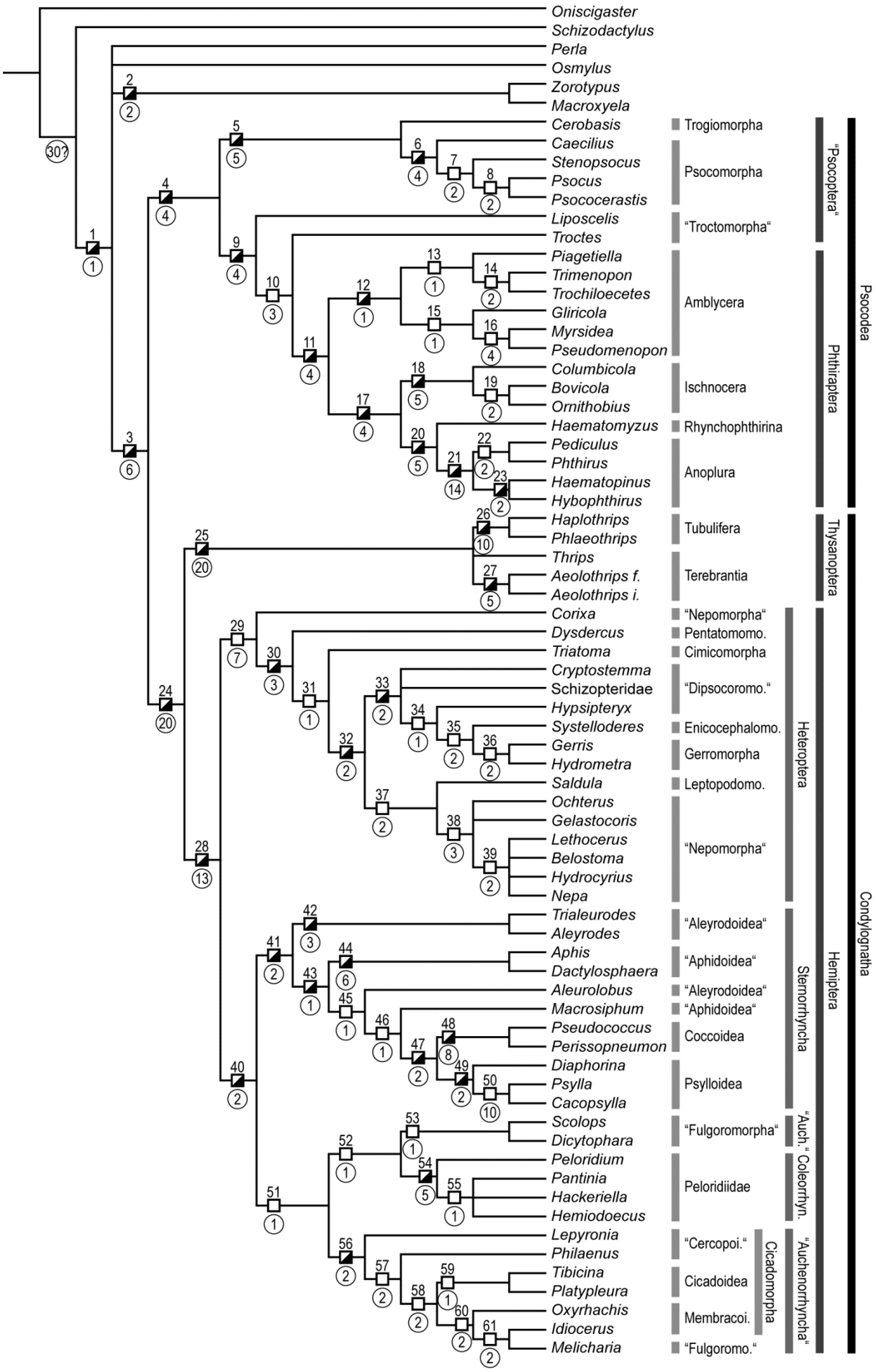
Oniscigaster
Schizodactylus
Perla
Osmylus
Zorotypus
Macroxyela
Cerobasis
Caecilius
Stenopsocus
Psocus
Psococerastis
Liposcelis
Troctes
Piagetiella
Trimenopon
Trochiloecetes
Gliricola
Myrsidea
Pseudomenopon
Columbicola
Bovicola
Ornithobius
Haematomyzus
Pediculus
Phthirus
Haematopinus
Hybophthirus
Haplothrips
Phlaeothrips
Thrips
Aeolothrips f.
Aeolothrips i.
Corixa
Dysdercus
Triatoma
Cryptostemma
Schizopteridae
Hypsipteryx
Systelloderes
Gerris
Hydrometra
Saldula
Ochterus
Gelastocoris
Lethocerus
Belostoma
Hydrocyrius
Nepa
Trialeurodes
Aleyrodes
Aphis
Dactylosphaera
Aleurolobus
Macrosiphum
Pseudococcus
Perissopneumon
Diaphorina
Psylla
Cacopsylla
Scolops
Dicytophara
Peloridium
Pantinia
Hackeriella
Hemiodoecus
Lepyronia
Philaenus
Tibicina
Platypleura
Oxyrhachis
Idiocerus
Melicharia
Trogiomorpha
Psocomorpha
"Troctomorpha"
Amblycera
Ischnocera
Rhynchophthirina
Anoplura
Tubulifera
Terebrantia
"Nepomorpha"
Pentatomomo.
Cimicomorpha
"Dipsocoromo."
Enicocephalomo.
Gerromorpha
Leptopodomo.
"Nepomorpha"
"Aleyrodoidea"
"Aphidoidea"
"Aleyrodoidea"
"Aphidoidea"
Coccoidea
Psylloidea
"Fulgoromorpha"
Peloridiidae
"Cercopoi."
Cicadoidea
Membracoi.
"Fulgoromo."
Cicadomorpha
"Psocoptera"
Phthiraptera
Thysanoptera
Heteroptera
Sternorrhyncha
"Auch."
Coleorrhyn.
"Auchenorrhyncha"
Hemiptera
Psocodea
Condylognatha

Figure A2 (previous page). Original strict consensus cladogram of 397 characters and 72 taxa (1375 steps, unambiguous only) calculated with TNT. Encircled numbers indicate Bremer Support values, which were calculated using TNT. Black-and-white boxes indicate homoplasious and non-homoplasious apomorphy-complexes, white boxes only non-homoplasious ones (apomorphies of single species not labeled). Homoplasious characters are set in *italics* (not identical with those in Figs. 28 and A1). **apomorphy-complex 1:** *(32/0)*, *(198/0)*, (231/0), (244/0), (265/0), (336/0), (379/2), (422/0), *(435/1)*. **2:** (9/3), *(46/0)*, *(47/0)*, *(336/1)*, *(364/1)*, *(384/1)*, *(436/1)*, *(500/0)*, *(510/1).* **3:** (71/0), *(154/0)*, (214/1), (215/1), *(218/0)*, (220/1), (230/0), (261/0), (264/0), (272/0), *(277/0)*, (302/1), *(309/0)*, *(341/0)*, *(384/1)*, (453/0). **4:** *(18/0)*, *(48/1)*, (143/1), *(153/1)*, *(198/1)*, (217/2), (232/1), (404/1), (407/1), (420/1), *(421/1)*, (454/1), *(474/0)*, *(490/1)*. **5:** *(37/1)*, *(247/0)*, *(262/0)*, (396/1), *(423/1)*, *(424/1)*. **6:** *(11/1)*, *(88/1)*, (144/1), *(217/1)*, *(269/0)*, (307/1). **7:** *(18/1)*, *(109/1)*, *(186/0).* **8:** *(32/1)*, *(123/1).* **9:** *(0/1)*, *(5/1)*, (24/0), *(41/1)*, *(109/1)*, *(288/0)*, (334/1), *(388/1)*, *(430/0)*, *(483/0)*, *(515/1).* **10:** *(34/0)*, *(111/0)*, *(201/0).* **11:** (24/2), *(48/0)*, *(143/0)*, *(186/0)*, (216/2), *(217/0)*, *(370/1)*, *(397/0).* **12:** *(119/1)*, *(126/1)*, (128/1), (235/1). **13:** *(279/1)*, *(302/0)*, *(453/1).* **14:** *(54/1)*, *(423/1)*, *(424/1)*, *(492/0).* **15:** *(422/1).* **16:** *(118/1)*, *(201/1)*, *(385/1)*, *(435/1)*, *(443/1).* **17:** *(33/1)*, *(96/0)*, (234/0), *(153/0)*, *(247/0)*, *(254/0)*, *(270/0)*, *(275/0)*, *(276/0)*, (305/0), *(490/0).* **18:** *(50/1)*, *(58/1)*, (64/1), *(118/1)*, (122/1), *(443/1)*, *(496/1).* **19:** *(201/1)*, *(435/1)*, *(444/0)*, *(484/1)*. **20:** *(24/3)*, *(44/0)*, *(46/1)*, *(65/1)*, *(105/0)*, *(109/0)*, (149/1), *(155/1)*, (166/1), *(172/0)*, (268/0), *(301/0)*, *(312/0)*, (369/1), *(420/0)*, (476/1). **21:** *(33/0)*, (66/1), (67/1), *(160/1)*, (168/3), (171/3), (179/1), *(183/1)*, (289/1), (313/1), (314/1), (316/1), *(317/0)*, (410/1), (411/1), (413/1), (415/1), *(436/1)*, (458/1). **22:** *(48/1)*, *(440/0)*, *(454/0)*, *(493/0)*. **23:** *(58/1)*, (102/1), (103/1), *(118/1)*, (252/1), (402/1), *(429/1)*. **24:** *(31/0)*, *(47/0)*, (59/0), *(65/1)*, *(89/0) (111/0)*, (168/1), (171/1), (193/1), (221/1), *(242/0)*, (256/1), *(266/0)*, *(269/0)*, *(274/0)*, *(275/0)*, *(276/0)*, *(332/0)*, (368/1), (382/1), (387/1), (392/1), *(394/0)*, (409/1), (419/1), *(427/0)*, (468/1), *(505/1)*. **25:** (4/1), *(37/1)*, (55/1), *(86/0)*, *(88/1)*, (106/1), (167/1), *(178/0)*, (236/1), *(263/3)*, *(280/1)*, *(283/1)*, *(370/1)*, (371/1), (372/1), *(379/0)*, (383/1), (390/1), (470/1), (482/1), *(486/0)*, *(493/0)*, *(517/1)*. **26**: *(54/0)*, (57/1), (176/1), *(203/1)*, *(255/0)*, (374/1), (379/1), *(381/1)*, (433/1), *(485/0)*, *(500/2)*, *(510/1).* **27:** *(32/1)*, *(230/1)*, *(264/1)*, *(272/1)*, (282/1), (318/0), *(336/1)*, *(488/0)*. **28:** *(10/0)*, *(19/1)*, (42/1), *(160/1)*, (162/0), (170/0), (175/1), (182/1), (189/1), *(254/0)*, *(270/0)*, (291/1), *(312/0)*, *(317/0)*, *(339/0)*, *(367/0)*, *(373/0)*, *(375/0)*, *(378/0)*, (389/0), (391/0), *(498/0)*, *(504/0)*. **29:** *(41/1)*, *(44/0)*, *(79/1)*, *(105/0)*, *(126/1)*, *(155/1)*, *(201/0)*, *(288/0)*, *(502/1).* **30:** *(40/1)*, *(137/1)*, (139/1), *(204/1)*, *(388/1)*, *(483/0)*, *(517/1)*. **31:** *(48/1)*, *(207/1)*. **32:** (190/1), *(292/2)*, *(342/1).* **33:** *(18/0)*, (138/2), *(493/0)*, *(502/0)*. **34:** *(40/0)*, *(56/1)*. **35:** *(138/1)*, *(298/1)*. **36:** *(60/1)*, *(218/1)*, *(256/0)*, *(502/1)*. **37:** *(33/1)*, *(47/1)*, *(300/1)*, *(471/1)*, *(490/1)*. **38:** *(119/1)*, *(120/1)*, *(139/0)*, *(218/1)*, *(293/1)*, *(298/1)*. **39:** *(18/0)*, *(190/2)*, *(207/0)*, *(256/0)*, *(518/1)*. **40:** *(76/0)*, (80/1), *(263/0)*, *(507/1).* **41:** *(109/1)*, *(154/1)*, *(178/0)*, *(181/0)*, *(206/0)*, (259/0), *(493/0)*, *(505/0)*. **42:** *(23/1)*, *(63/0)*, (284/1), *(342/1)*, *(356/1)*. **43:** *(263/1)*, *(357/1)*, *(506/0).* **44:** *(153/1)*, *(226/1)*, (348/1), (350/1), *(353/1)*, (447/1), (449/1), *(490/1)*. **45:** *(78/1)*, *(96/0)*, *(158/1)*, *(159/1)*, *(259/1)*, *(283/1)*, *(295/1)*. **46:** *(76/1)*, *(343/0)*, *(362/1)*. **47:** (81/1), (187/2), (324/1), *(352/0)*, (354/1). **48:** (7/1), *(18/0)*, *(24/3)*, *(86/0)*, *(206/1)*, *(257/0)*, *(258/0)*, *(353/1)*, (355/1). **49:** (28/1), (30/2), *(47/1)*, *(78/0)*, *(189/0)*, *(208/0)*, (290/1). **50:** *(45/0)*, *(56/0)*, *(79/1)*, *(96/1)*, *(226/1)*, *(283/0)*, *(292/1)*, *(295/0)*, *(345/0)*, *(351/0)*, *(441/2)*, *(446/1)*, *(490/1).* **51:** *(344/0)*, *(521/0)*. **52**: *(48/1)*, *(120/1)*, *(258/0)*. **53:** *(44/0)*, *(125/1)*, *(201/0)*. **54:** (2/1), (6/1), (8/1), (30/1), *(119/1)*. **55:** *(18/0)*. **56:** (121/1), (155/2), *(181/1)*, *(280/1)*. **57:** *(37/1)*, *(63/0)*, *(204/1)*, *(490/1)*, *(494/1)*, *(495/1)*. **58:** *(48/1)*, *(158/1)*, *(159/1)*. **59:** *(10/1)*, *(19/0)*, *(47/1)*. **60:** *(32/1)*, *(259/1)*, *(280/0)*. **61:** *(63/1)*, *(295/1)*, *(378/1)*.

8.3 Appendix3: List of characters not included in the cladistic analysis

3 anterior part of head capsule (i.a. clypeus, genae, postmentum) elongated to from a rostrum (Mey 2005): (0) absent; (1) present. This character is apparently an autapomorphy of *Haematomyzus* (Weber 1969).

14 unpaired ventral cervical sclerite: (0) absent; (1) present. The presence of an unpaired ventral cervical sclerite is apparently an autapomorphy of *Zorotypus* (Friedrich & Beutel 2008).

15 cervical apodemes (Vilhelmsen 2000): (0) absent; (1) present. The presence of cervical apodemes is apparently an autapomorphic character of *Macroxyela* (Vilhelmsen 2000).

16 laterocervicalia and propleura fused (propectus) (Vilhelmsen 2000): (0) absent; (1) present. The propectus is an autapomorphic character of *Macroxyela* (Vilhelmsen 2000).

17 preocular slit (see fig. 50 of Symmons 1952): (0) absent; (1) present. The presence of the preocular slit in the present study is an autapomorphy of *Piagetiella* (Figs. 19A,B).

22 compound eyes: (0) absent; (1) present. The absence of the compound eyes is a potential autapomorphy of *Hybophthirus* (Tröster 1990a). Young (1953) gave additional information concerning the functionality of the compound eye of *Haematopinus.*

25 type of ommatidium (see also Kuhn [1926] for Heteroptera, Cicadomorpha; Jentsch [1940] for Psocoptera; Wundrig [1936] for Liposcelididae): (0) eucon (crystalline cone present within cells, typical compound eye); (1) acon (crystalline cone absent). This character is not included in the cladistic analysis as original information to the ocular cellular structure is very fragmentary.

26 lens of ommatidia equiped with an iris-like cuticular ring: (0) absent; (1) present. This character is not included in the cladistic analysis as original information to the ocular cellular structure is very fragmentary or not explicitly mentioned. However, the iris-like cuticular ring is apparently an autapomorphy of Amblycera (Stöwe 1943).

27 number of lenses per eye (character of Wundrig [1936] and Mey [2005]): (0) 2; (1) 1; (2) more than 2. This character is not included in the cladistic analysis as original information to the ocular cellular structure is very fragmentary or not explicitly mentioned.

39 second pair of cones formed by clypeus (cc2) (Fig. 27,D): (0) absent; (1) present. "Lippentaster" of *Phthirus* (Hirsch 1986).

49 clypeolabral ridge (separates clypeus from labrum): (0) absent; (1) present. The absence of the clypeolabral ridge in *Nepa* (Hamilton 1931) is apparently an autapomorphic character.

51 morphology of pulvinus (Smith 2001): (0) simple lobe with complete ventral carina ("band of sclerotization that extends from the mandibular frame-work to support the pulvinus laterally"); (1) pulvinus separated into two lateral lobes with interrupted ventral carina. The simple lobe of *Bovicola* (see Smith 2001) is interpreted as an autapomorphy of this taxon.

52 marginal pulvinal bars (Symmons 1952; Smith 2001) or “Pulvinarsklerite” (Haub 1983) as "chitinious bar or thickening of the clypeal edge on either side of the pulvinus serves to support the lateral lobes of [the pulvinus], unlike the tormae they bear no muscles" (Symmons 1952): (0) absent; (1) present

53 anterior edge of pulvinus equipped with a crescent-shaped protrusion (Haub 1971) or anterior head margin with osculum (Smith 2001): (0) absent; (1) present. The presence of a pulvinar crescent-shaped protrusion is an autapomorphy of *Ornithobius* (Haub 1971).

61 origin of cephalic trichobothria: (0) in a deep, pitlike depression; (1) in a less developed depression. The cephalic trichobothria of Gerromorpha originate in deep depressions, whereas those of *Saldula* (Parsons 1962) are more flattened.

62 six lateral protuberances equipped each with a hair-like sensillum: (0) absent; (1) present. The presence of these exosceletal protuberances in *Phlaeothrips* (Mickoleit 1963) is considered as an autapomorphy.

68 cervical gland(s) ("Large asymmetric glands […] are present in the neck region between the suboeso-phageal complex and the oesophagus. They are connected with a sclerotized tube which opens dorsomedially on the posterior head capsule." Beutel & Weide 2005): (0) absent; (1) present. The presence of cervical glands is a potential autapomorphy of *Zorotypus* (Beutel & Weide 2005). Males of the genera *Merothrips* (Merothripidae, Terebrantia, Thysanoptera) are characterized by a structure resembling the cervical gland. It is located near the vertex ("Vertexdrüse") and secretes through its perforated surface (Moritz 2006). However, the homology is far from being settled.

72 Idlm4, M. cervico-occipitalis dorsalis: (0) absent; (1) present. The presence of Idlm4, M. cervico-occipitalis dorsalis is apparently an autapomorphy of *Zorotypus* (Friedrich & Beutel 2008).

74 Idvm2, M. cervico-occipitalis medialis: (0) absent; (1) present. The presence of Idvm2, M. cervico-occipitalis medialis is apparently an autapomorphy of *Zorotypus* (Friedrich & Beutel 2008).

75 Idvm3, M. cervico-occipitalis posterior: (0) absent; (1) present. The presence of Idvm3, M. cervico-occipitalis posterior is apparently an autapomorphy of *Zorotypus* (Friedrich & Beutel 2008).

85 Idvmx5, “M. sterno-cervicalis”: (0) absent; (1) present. The presence of Idvmx5, “M. sterno-cervicalis” is apparently an autapomorphy of *Haematomyzus* (Weber 1969).

87 Itpm2, M. propleuro-occipitalis: (0) absent; (1) present. The presence of Itpm2, M. propleuro-occipitalis is apparently an autapomorphy of *Zorotypus* (Friedrich & Beutel 2008).

90 Ipcmx1, “M. coxa-cervicalis secundus”: (0) absent; (1) present. The presence of Ipcmx1, “M. coxa-cervicalis secundus” is apparently an autapomorphy of *Haematomyzus* (Weber 1969).

91 Ipcmx2, “M. coxa-cervicalis tertius”: (0) absent; (1) present. The presence of Ipcmx2, “M. coxa-cervicalis tertius” is apparently an autapomorphy of *Haematomyzus* (Weber 1969).

92 Ipcmx3, “M. coxa-cervicalis quartus”: (0) absent; (1) present. The presence of Ipcmx3, “M. coxa-cervicalis quartus” is apparently an autapomorphy of *Haematomyzus* (Weber 1969).

93 Ipcmx4, “M. coxa-cervicalis quintus”: (0) absent; (1) present. The presence of Ipcmx4, “M. coxa-cervicalis quintus” is apparently an autapomorphy of *Haematomyzus* (Weber 1969).

95 Ivlm2, M. submento-cervicalis: (0) absent, (1) present. The presence of Ivlm2, M. submento-cervicalis is apparently an autapomorphy of *Perla* (Chisholm 1962).

98 Ivlmx2: (0) absent; (1) present. The presence of Ivlmx2 is apparently an autapomorphy of *Perla* (Chisholm 1962).

99 Idx1, “M. cervico-cervicalis”: (0) absent; (1) present. The presence of Idx1, “M. cervico-cervicalis” is apparently an autapomorphy of *Haematomyzus* (Weber 1969).

100 Idx2, “Mxy”: 0) absent; (1) present. The presence of Idx2 is apparently an autapomorphy of *Zorotypus* (Beutel & Weide 2005).

104 Lig6 of Tröster (1990a), extends from ventral side of head capsule to "Vorderrand des ventralen Horizontalseptum" near piercer sheath: (0) absent; (1) present. For character state of *Haematopinus* see Tröster (1990a, p. 20). The presence of ligament 6 is apparently an autapomorphy of *Hybophthirus* (Tröster 1990a).

110 posterior tentorial arms equipped medioventrally with an elongated cone directed caudally ("Trabecula tentorii" of Staniczek 2001): (0) absent; (1) present. The presence of posttentorial cones is apparently an autapomorphy of *Oniscigaster* (Staniczek 2001).

114 posttentorium collar-like: (0) absent; (1) present. The presence of a collar like posterior tentorium is apparently an autapomorphy of *Macroxyela* (Beutel & Vilhelmsen 2007).

116 apodemal connection between corpotentorium and head capsule (excluding arms of tentorium): (0) absent; (1) present. This additional connection is apparently an autapomorphic character of *Scolops* (Kramer 1950).

117 Processus paratentorialis (Staniczek 2001) (cranial process located on ventrolateral margin of anterior tentorial pit): (0) absent; (1) present. The presence of the processus paratentorialis is apparently an autapomorphy of *Oniscigaster* (Staniczek 2001).

124 trabeculum (tra) (Figs. 21A,B) ("[…] lobe shaped structure arising predominately from the anterior margin of the antennal socket and may be continuous with the anterior margin of the head." Smith 2001): (0) absent; (1) present. The presence of the trabecula is apparently a synapomorphy of *Columbicola* and *Philopterus ornatus* (NITZSCH, 1866) (Smith 2001).

130 basiflagellite equipped with R-Structure (character of Zrzavý, 1990): (0) absent; (1) present. This character is not included in the cladistic analysis as it is uncertain if all authors really analyzed the ultrastructure of the antenna.

131 type of R-structure of basiflagellite (character of Zrzavý, 1990): (0) Bf(RVI); (1) Bf(RI). This character is not included in the cladistic analysis as it is uncertain if all authors really analyzed the ultrastructure of the antenna.

132 distiflagellite equipped with R-Structure (character of Zrzavý, 1990): (0) absent; (1) present. This character is not included in the cladistic analysis as it is uncertain if all authors really analyzed the ultrastructure of the antenna.

133 type of R-structure of distiflagellite (characters of Zrzavý, 1990): (0) Df(RVI); (1) Df(RV); (2) Df(RI). This character is not included in the cladistic analysis as it is uncertain if all authors really analyzed the ultrastructure of the antenna.

140 "Sensorien" (sensory organs situated laterad on at least third and fourth antennal segment): (0) absent; (1) present. This character is not included in the cladistic analysis as it is uncertain if all authors really analyzed the ultrastructure of the antenna. The "Rhinarium" of *Dactylosphaera* (Rilling 1960) is only figured but not explained in text which impedes its homology.

141 structure of "Sensorien": (0) flat kidney-shaped pad; (1) bi-lobed cone; (2) single-lobed cone. This character is not included in the cladistic analysis as it is uncertain if all authors really analyzed the ultrastructure of the antenna.

145 antennomeres three and four equipped each with scales arranged circularly: (0) absent; (1) present. This character is not included in the cladistic analysis as it is uncertain if all authors really analyzed the ultrastructure of the antenna.

146 antennomere four equipped with four cone-like chemoreceptors: (0) absent; (1) present. This character is not included in the cladistic analysis as it is uncertain if all authors really analyzed the ultrastructure of the antenna.

151 0an1, M. tentorioscapalis anterior: (0) absent; (1) present

152 0an2, M. tentorioscapalis posterior: (0) absent; (1) present

156 0an6, M. scapopedicellaris lateralis: (0) absent; (1) present

157 0an7, M. scapopedicellaris medialis: (0) absent; (1) present

164 classification of secondary or anterior articulation of dicondylic mandible: (0) anterior articulation between basal margin of clypeus and basal margin of mandible; (1) anterior articulation partly between basal margin of clypeus and shifted proximad from basal margin of mandible or anterior articulation as functional complex between processus paratentorialis (paratentorial jaw) and basal margin of mandible. The paratentorial jaw is apparently an autapomorphy of *Oniscigaster* (Staniczek 2001).

165 mandibles rotated 180° or mandibles operate laterally not medially (Weber 1969): (0) absent; (1) present. This character is not applicable for Hemiptera as the mandibular stylets are highly flexible and can work laterally and medially (see pathways of salivary sheaths). Nevertheless, the mandibles rotated 180° are an autapomorphy of *Haematomyzus* (Weber 1969).

169 plate-like part of divided mandible ("schwenkbare Mandibelplatte", Ramcke 1965) equipped with an apodeme ("Apodem des sekundären Mandibelgelenkes", Ramcke 1965) directed craniad: (0) absent; (1) present. The absence of the apodeme of the mandibular jaw within Anoplura in *Hybophthirus* (Tröster 1990a) is an autapomorphic character.

174 prostheca: (0) on both mandibles; (1) only on the left mandible

180 mandibles fused completely or partly ("Blutüberleitsklerite" if applicable) with hypopharynx (Tröster 1990a): (0) absent; (1) present. The fusion of the mandibles with the hypopharynx is at least an apomorphic character of *Haematopinus* (Tröster 1990a). However, Hirsch (1986) considered this character for *Phthirus* as “das läßt sich hier nicht eindeutig festlegen".

191 mandibular gland: (0) absent; (1) present. This character is not included in the cladistic analysis as it is uncertain if all authors really analyzed all the softparts associated with the mandible. The ground plan character of Hemiptera is unclear as, however, mandibular glands were documented at least for *Oncopeltus* (Lygaidae, Pentatomomoprha) (Linder 1956) and *Aphididae* (Saxena & Chada 1971).

192 number of mandibular glands: (0) two, arranged bilateral symmetrically; (1) only developed on left side of body. This character is not included in the cladistic analysis as it is uncertain if all authors really analyzed all the softparts associated with the mandible.

202 0md7, tentoriomandibularis medialis superior: (0) absent, (1) present. The presence of 0md7 is apparently an autapomorphy of *Oniscigaster* (Staniczek 2001).

211 0mdx6, retractor of mandible in Hemiptera: (0) absent, (1) present. The presence of this additional mandibular retractor is apparently an autapomorphy of *Platypleura* (Singh 1971).

212 0mdx7, retractor of mandible in Hemiptera: (0) absent, (1) present. The presence of this additional mandibular retractor is apparently an autapomorphy of *Dactylosphaera* (Rilling 1960).

227 maxillary dendritic canal (mxc) (e.g. Figs. 12B, 14B): (0) absent; (1) present. Backus (1985) mentioned "stylet sensory organs have been found in all hemipterans examined". In the group Coleorrhyncha this is confirmed for *Peloridium* (Cobben 1978) and *Xenophyes* (Brozek 2007). Hunter & Ullman (1992) documented the maxillary dendritic canal for *Frankliniella.* However, this character is presently not included in the cladistic analysis as it is uncertain if all authors really analyzed the ultrastructure of the laciniae.

228 number of maxillary dendritic canals per stylet (e.g. Figs. 12B, 14B) (see also Backus 1985): (0) 1; (1) 2. Hunter & Ullman (1992) documented four dendritic canals for *Frankliniella.* However, this character is presently not included in the cladistic analysis as it is uncertain if all authors really analyzed the ultrastructure of the laciniae.

229 number of dendrites per both maxillary dendritic canals (see also Backus 1985): (0) 2; (1) 3; (2) 5. Hunter & Ullman (1992) documented four dendrites for *Frankliniella.* However, this character is presently not included in the cladistic analysis as it is uncertain if all authors really analyzed the ultrastructure of the laciniae.

237 stipes equipped with a groove and a clamp as guiding device for lacinia (see also fig. 5 of Noland 1924): (0) absent; (1) present. The stipital guiding device for the lacinia is apparently an autapomorphy of *Troctes* (Noland 1924).

238 stipes subdivided longitudinally ("juxtastipes" and "verastipes" of Khattar 1958): (0) absent; (1) present. The longitudinal subdivision of the stipes is apparently an autapomorphic character of *Schizodactylus* (Khattar 1958).

239 interlocking of maxillary plates (stipites) with each other: (0) absent; (1) present. The interlocking of the maxillary plates is apparently an apomorphy of *Psylla* (Weber 1929a) or Psylloidea.

240 interlocking of maxillary plates (stipites) with mesal edges of anteclypeus: (0) absent; (1) present. This locking mechanism is apparently an autapomorphy of *Dictyophara* (Figs. 14A,B).

241 interlocking of maxillary plates (stipites) with labrum ("Druckknöpfe" of Rilling 1960): (0) absent; (1) present. This locking mechanism is apparently an autapomorphy of *Dactylosphaera* (Rilling 1960).

243 apices of galea and lacinia, respectively, forming a functional unit acting as a scraping device (Staniczek 2001): (0) absent; (1) present. The maxillary scraping device is apparently an autapomorphy of *Oniscigaster* (Staniczek 2001).

246 galea inserted on subgalea (Beutel et al. 2010): (0) absent; (1) present. The insertion of the galea on the subgalea is apparently an autapomorphy of *Osmylus* (Beutel et al. 2010). Khattar (1958) used "subgalea" and "basigalea" for the same structure in *Schizodactylus*.

248 dorsal part of galea equipped with a longitudinal groove medially (von Kéler 1966a, "praeorale Nahrungsrinnen-Sklerite" or "Blutüberleitrinne" of Tröster 1990a): (0) absent; (1) present (right

galea forms a canal with ventral part of fulcrum [if applicable], supported by left galea ventrolaterally, Tröster 1990a). The longitudinal galeal groove is apparently an autapomorphy of *Hybobphthirus* (Tröster 1990a).

250 lateral membranous connection between galea (i.a. longitudinal grooves, if applicable) and dorsal part of mandible (Tröster 1990a): (0) absent; (1) present. The galeal-mandibular connection is apparently an autapomorphy of *Hybophthirus* (Tröster 1990a).

260 maxillary glands (mxg) (Fig. 12B) (cephalic glands): (0) absent; (1) present. The homology of the "compact gland tissue […] between the extrinsic tentorial muscles of the maxilla" of *Osymlus* is unclear (Beutel el. 2010). The nomenclature of Chisholm (1962) applied for *Perla* is somewhat confusing. In the text the term "maxillary gland" is used (paired gland with common duct entering salivarium) which is, however, abbreviated with "H.S.G" standing for "hypopharyngeal salivary gland". "Maxillo-Mandibulardrüsen" of *Dactylosphaera* (Breider 1952). Secretory cells of *Caecilius* and *Liposcelis* present at the lever of the lacinia entering the head capsule and protrude into the galea are likely homologous to the maxillary gland. "Laciniadrüse" of *Pseudomenopon* (Haub 1967); "Pawlowski-Drüse" of *Haematopinus* (Ramcke 1965); “Kopfspeicheldrüse” of *Haematomyzus* (Weber 1969). This character is not included in the cladistic analysis as it is uncertain if all authors really analyzed all the softparts associated with the maxilla.

262 0mx2, M. craniolacinialis: (0) absent; (1) present. The absence of 0mx2, M. craniolacinialis is apparently an autapomorphy of *Haematomyzus* (Weber 1969).

294 tube-like labium equipped with labial intercalary sclerites located each between first and second labial segment (two pairs) and third and fourth labial segment: (0) absent; (1) present. The presence of three pairs of labial intercalary sclerites is apparently an autapomorphy of *Gelastocoris* (Parsons 1958).

296 "Mandibularbuerste" referring to tube-like labium: (0) absent; (1) present (Barth 1953a,b). This brush-like device is apparently an autapomorphy of *Triatoma* (Barth 1953a,b).

306 number of paraglossae: (0) 2; (1) 1

311 character of mentum: (0) membranous; (1) sclerotized. “sclerite of postmentum” of *Psocus* (Cope 1940).

315 limes labialis equipped with two apodemes caudally: (0) absent; (1) present. "Apodem der Stilettsacklasche" of *Haematopinus* (Ramcke 1965). The absence of the apodemes of the limes labialis is apparently an autapomorphy of *Hybophthirus* (Tröster 1990a).

319 sclerotized plate at base of labial palp, can be abducted: (0) absent; (1) present. "Labialschuppe" of *Haematomyzus* (Weber 1969). The presence of the movable plate at the base of the labial palp is apparently an autapomorphy of *Haematomyzus* (Weber 1969).

320 four pairs of labial barbs: (0) absent; (1) present. "ventraler Haken 1,2,3,4" of *Haematomyzus* (Weber 1969). The presence of labial barbs is apparently an autapomorphy of *Haematomyzus* (Weber 1969).

321 hollow cone in border region of pre- and postmetum directed backwards, not homologous with labial palps, acting as "security hooks" (Haub 1983): (0) absent; (1) present. The presence of this labial labial cone is apparently an autapomorphy of *Trochiloecetes* (Haub 1983).

322 sensilla at apex of labial rostrum (including paraglossa and glossa) (for *Ochterus*, *Gelastocoris*, and *Lethocerus* see Brozek [2008]): (0) absent; (1) present. This character is not included in the cladistic analysis as it is uncertain if all authors really focused on the ultrastructure of the labium.

323 sensilla grouping: (0) irregular/two fields; (1) two rows; (2) three groups; (3) eight pairs; (4) two fields with four sensilla each. This character is not included in the cladistic analysis as it is uncertain if all authors really focused on the ultrastructure of the labium.

327 "Stacheldrüse" (von Kéler 1966a, Tröster 1990a), glandular cells on dorsal base of prementum (see also Tröster 1990a for *Bovicola*): (0) absent; (1) present. This character is not included in the cladistic analysis as it is uncertain if all authors really analyzed all the softparts associated with the labium.

328 opening of "Stacheldrüse" (Tröster 1990a): (0) into salivary duct; (1) between lateral sclerites of piercer sheath. This character is not included in the cladistic analysis as it is uncertain if all authors really analyzed all the softparts associated with the labium.

329 0la2, M. postoccipitoglossalis lateralis: (0) absent; (1) present. The presence of 0la2, M. postoccipitoglossalis lateralis is apparently an autapomorphy of *Perla* (Chisholm 1962).

349 0lax7, labial abductor of Hemiptera: (0) absent; (1) present

358 0lax15, labial muscle of Hemiptera: (0) absent; (1) present. The presence of the labial muscle 0lax15 is apparently an autapomorphy of *Lethocerus* (Parsons 1968).

363 0lax20, labial muscle of Hemiptera: (0) absent; (1) present. The presence of 0lax20 is apparently an autapomorphy of *Perissopneumon* (Singh 1971).

365 0lax22, “M. palpopalpalis labii primus anterior”: (0) absent; (1) present. The presence of a third intrinsic muscle of the first labial palpomere is apparently an autapomorphy of *Oniscigaster* (Staniczek 2001).

386 cibarial sense organ (cbs) (Fig. 22F) (composed of a few cells and located laterad/ventrad to cibarial sclerite [Buckup 1959] or ventrad cibarial fenestrations [Haub 1967]): (0) absent; (1) present. This character is not included in the cladistic analysis as it is uncertain if all authors really analyzed all the softparts associated with the hypopharynx.

395 oral hypopharyngeal arms equipped each with a clamp-like or Y-shaped structure: (0) absent; (1) present. “Lingualsklerit 1 + 2” of *Bovicola* (Risler 1951). The presence of a clamp-like structure on the oral hypopharyngeal arms is apparently an autapomorphy of Trichodectidae (Risler 1951; Haub 1972).

401 structure of entity of posterior (Matsuda 1965) hypopharyngeal arms: (0) blunt distal apex connected with "Chitinfaden"; (1) bi-furcated stylet-like protrusion with free distal apex; (2) blunt apex

406 tendons attached to each ovoidal sclerite ("Hypopharynxretraktorsehne") (apov) (e.g. Figs. 7A–C): (0) free; (1) connected with each other by a chitinous clamp. “Chitinspange” of *Bovicola* (Risler 1951, p. 343). The connection between both tendons of the ovoidal sclerites is an autapomorphy of *Bovicola* (Risler 1951).

412 floor of "Preoralhöhle" strengthened by a crescent-shaped "Stützelement" (Tröster 1990a): (0) absent; (1) present. The presence of a strengthened preoral cavity is apparently an autapomorphy of *Hybophthirus* (Tröster 1990a).

414 structure of median salivary stylet (Fig. 26C): (0) opened ventrally; (1) closed (Tröster 1990a). The non-closed salivary stylet is apparently an autapomorphy of *Hybophthirus* (Tröster 1990a).

418 number of valves: (0) 0; (1) at least 1 at border region of salivarium and affarent salivary duct; (2) 2; (3) 3. This character is not included in the cladistic analysis as it is uncertain if all authors really analyzed the ultrastructure of the hypopharynx.

425 distal wall of hypopharynx equipped with lobe-like folds to seal half-pipe of epipharynx during transporting blood into preoral cavity: (0) absent; (1) present. The presence of hypopharyngeal folds associated with the epipharynx is apparently an autapomorphy of *Trochiloecetes* (Haub 1983).

426 corpora labialia (paired globular glands without lumen and efferent duct(s) situated anterad subesophageal ganglion, Buckup 1959) (cl) (Figs. 20H, 22G): (0) absent; (1) present. “dritte und kleinste Anteil der Labialdrüse“ of Tubulifera (Mickoleit 1963); "Drüsen im Hypopharynx" of *Ornithobius* (Haub 1971); for character state of *Gliricola* see Strindberg (1916) in Haub (1967); "fragliches Organ" of *Haematomyzus* (Weber 1939, 1969) is similar in shape and position to the corpora labialia, and thus considered as homologous. This character is not included in the cladistic analysis as it is uncertain if the focus of all authors was also on the softparts associated with the hypopharynx.

439 0hy10, M. loroloralis: (0) absent; (1) present. The presence of 0hy10, M. loroloralis is a potential autapomorphy of *Oniscigaster* (Staniczek 2001).

445 0hyx3, muscle of the hypopharyngeal wing in Hemiptera: (0) absent; (1) present. The presence of 0hyx3 is a potential autapomorphy of *Platypleura* (Singh 1971).

448 0hyx6, “M. hypopharyngo salivaris quartus”: (0) absent; (1) present. The presence of 0hyx6 is apparently an autapomorphy of *Aphis* (Weber 1928).

450 0hyx8, “M. hypopharyngo salivaris sextus”: (0) absent; (1) present. The presence of 0hyx8 is apparently an autapomorphy of *Aphis* (Weber 1928).

451 0hyx9, “Msusph”: (0) absent; (1) present. The presence of 0hyx9 is a potential autapomorphy of *Osymlus* (Beutel et al. 2010).

452 epipharyngeal sense organ (eps) (Figs. 12A,C, 13B, 14B): (0) absent; (1) present. This character is not included in the cladistic analysis as it is uncertain if all authors really focused on the ultrastructure or soft parts of the labrum. “oral sense organ” of *Schizodactylus* (Khattar 1958).

460 precibarial valve (prev) (Fig. 13F) (see also Backus & McLean 1982; Backus 1985; Hunter & Ullman 1994): (0) absent; (1) present. This character is not included in the cladistic analysis as it is uncertain if all authors really focused on the ultrastructure of the epipharynx.

461 morphology of precibarial valve (see also Ullman & McLean 1986; Hunter & Ullman 1994): (0) bulbous with a deep central suture; (1) flap-like, folded, unhinged; (2) flap-like, hinged; (3) simple lobe. This character is not included in the cladistic analysis as it is uncertain if all authors really focused on the ultrastructure of the epipharynx.

462 function of precibarial valve (see also Ullman & McLean 1986; Hunter & Ullman 1994): (0) valve closes against valve receptacle; (1) valve closes opening of cibarium. This character is not included in the cladistic analysis as it is uncertain if all authors really focused on the ultrastructure of the epipharynx.

463 number of pre- and cibarial sensilla of the epipharyngeal sense organ (see also Ullman & McLean 1986; Hunter & Ullman 1994; Hunter et al. 1996): (0) 16; (1) 18; (2) usually 20; (3) 24; (4) 12; (5) 10; (6) 6. This character is not included in the cladistic analysis as it is uncertain if all authors really focused on the ultrastructure of the epipharynx.

464 number of distal precibarial sensilla, D-sensilla (see also Ullman & McLean 1986; Hunter & Ullman 1994): (0) 8; (1) 10; (2) usually 10; (3) 4. This character is not included in the cladistic analysis as it is uncertain if all authors really focused on the ultrastructure of the epipharynx.

465 number of P-sensilla (see also Ullman & McLean 1986; Hunter & Ullman 1994): (0) 8; (1) 6; (2) 18; (3) 2. This character is not included in the cladistic analysis as it is uncertain if all authors really focused on the ultrastructure of the epipharynx.

466 arrangement of distal precibarial sensilla (see also Ullman & McLean 1986; Hunter & Ullman 1994): (0) single row, unpaired papillae; (1) alternating paired and unpaired papillae; (2) usually paired groups. This character is not included in the cladistic analysis as it is uncertain if all authors really focused on the ultrastructure of the epipharynx

467 morphology of precibarial chemosensilla (see also Ullman & McLean 1986; Hunter & Ullman 1994): (0) oval, raised papillae; (1) D-sensilla of two types: unpaired oval, raised papillae; paired, oval, concave papillae. Paired oval, slightly raised P-sensilla; (2) D-sensilla of two types: round and oval, both types raised. P- and H-sensilla rounded; (3) D-sensilla tube-like, P-sensilla as papillae. (see character 466)

475 anterior part of cibarium elongated to form a tube: (0) absent; (1) present. "Cibarialrohr" of *Haematomyzus* (Weber 1969). The presence of the elongated cibarium is a potential autapomorphy of *Haematomyzus* (Weber 1969).

477 "Mundvorraum" forming two pads for sealing injection side: (0) absent; (1) present. "Polster" of *Haematomyzus* (Weber 1969). The presence of these pads is a potential autapomorphy of *Haematomyzus* (Weber 1969).

479 "palatale Falte"/Epiglottis (von Kéler 1966a), formed by dorsal wall of pharynx: (0) absent; (1) present. "Kehldeckel" of *Hypbophthirus* (Tröster 1990a). The presence of this fold is a potential autapomorphy of *Hybophthirus.*

481 lateral walls of pharynx sclerotized and equipped with sclerotized teeth directed caudad: (0) absent; (1) present. "Pharynx-Zähnchen" of *Hybophthirus* (Tröster 1990a). The presence of pharyngeal teeth is apparently an autapomorphy of *Hybophthirus* (Tröster 1990a).

487 0bu2, M. frontobuccalis anterior: (0) absent; (1) present

501 principal salivary gland ("basophile dorsale Labialdrüse", Haug 1952): (0) absent; (1) present. Unclear character state for *Macroxyela* as the statement “The small, tube-like salivary glands” (Beutel & Vilhelmsen 2007) allows no specification towards principal or accessory salivary gland. The character is also unclear for *Osmylus*: "Large, sac-like reservoirs of the salivary glands are present in the posterior head region lateral, dorsal and ventral to the posterior pharynx" (Beutel et al. 2010). This description is not sufficient for the classification of the salivary gland complex. ”one pair in prothorax” of *Perla* (Chisholm 1962). The subsidiary gland of *Nepa* (Hamilton 1931) is interpreted as the second lobe of the regularly bilobed principal salivary gland (see also Cobben 1978), and the salivary reservoirs as the accessory glands. “Sp2” of

Aphis (Weber 1928). The character is unclear for *Psocus* as Cope (1940) described just as single set of salivary glands which impedes the homology to either the principal or accessory salivary gland. ”glande labial dorsale” of *Stenopsocus* (Badonnel 1934); “Dorsaldrüsen” of *Myrsidea* (Buckup 1959); unclear character state for *Piagetiella* as only one pair of salivary glands is visible in section series; “Ventraldrüsen” of *Trimenopon* (Stöwe 1943); unclear character state for *Columbicola* as the salivary glands are not visible in the sectioned part of the specimen, this is also applicable for *Pediculus*; “thorakale Speicheldrüsen” of *Haematomyzus* (Weber 1969).

503 accessory gland (Miyamoto 1961) ("acidophile ventrale Labialdrüse", Haug 1952): (0) absent; (1) present. “Receptacle” of *Schizodactylus* (Khattar 1972); “one in the mesothorax” of *Perla* (Chisholm 1962); “glande labiale ventrale" of *Stenopsocus* (Badonnel 1934); “Ventraldrüse” of *Myrsidea* (Buckup 1959); “Dorsaldrüse” of *Trimenopon* (Stöwe 1943). Unclear character state for *Haematomyzus* (Weber 1969) as only one salivary or labial gland, respectively, is described in the text of Weber (1969). However, the "thorakale Speicheldrüse" is equipped in its anterior region with globuli likely representing a second gland.

509 "traubenförmige Drüse" of von Kéler (1966a), leading to "Speichelhöhle" and dorsad opening of maxillary gland: (0) absent; (1) present. The presence of this gland is a potential autapomorphy of *Hybophthirus* (Tröster 1990a).

511 0hyx10, “M. intersalivarius”: (0) absent; (1) present. The presence of a muscle connecting both afferent salivary ducts is a potential autapomorphy of *Aeolothrips fasciatus* (Mickoleit 1963).

512 0hyx11, “M. salivarii longitudinales”: (0) absent; (1) present. The presence of the longitudinal muscles of the wall of the salivarium is apparently an autapomorphy of *Haematomyzus* (Weber 1969).

513 0hyx12, “M. hypopharyngo salivaris septus”: (0) absent; (1) present. The presence of 0hyx12, “M. hypopharyngo salivaris septus” is a potential autapomorphy of *Schizodactylus* (Khattar 1964).

514 proto-, deuto- and tritocerebrum fused to a single mass: (0) absent; (1) present

519 frontal ganglion: (0) distinguishable; (1) not distinguishable. This character is not included in the cladistic analysis. The frontal ganglion is a minute structure, especially in minute specimens (e.g. *Troctes* in Noland 1924), and often attached to the brain. It cannot be excluded that it was overlooked in primarily older studies (e.g. Weber 1935).

520 hypocerebral ganglion: (0) distinguishable; (1) not distinguishable. This character is also not included in the cladistic analysis (see character 519).

9. Lebenslauf

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07/2011 – 04/2012	Friedrich-Schiller-Universität Jena Publikation zur Diplomarbeit: „The male postabdomen and reproductive system of *Bibio marci* Linnaeus, 1758 (Hexapoda: Diptera: Bibionidae)”; Vorarbeiten/Recherche zur Promotion
05/2012 – (07/2014)	Promotion zum Thema: „The evolution of head structures in Acercaria (Insecta)”.

Praktika

02/2009 – 04/2009	Museum für Naturkunde Chemnitz u. a. Aufbau einer Hauptsammlung „Schmetterlinge“, Datenaufnahme und Datenbankpflege, Sammlungspflege

10. Liste wissenschaftlicher Veröffentlichungen

Spangenberg R, Hünefeld F, Schneeberg K, Beutel RG (2012). The male postabdomen and reproductive system of *Bibio marci* LINNAEUS, 1758 (Hexapoda: Diptera: Bibionidae). Journal of Zoological Systematics and Evolutionary Research 50(4), 264–288.

Friedemann K, **Spangenberg R**, Yoshizawa K, Beutel RG (2013). Evolution of attachment structures in the highly diverse Acercaria (Hexapoda). Cladistics 2013, 1–32.

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Spangenberg R, Friedemann K, Weirauch C, Beutel RG (2013b): The head morphology of the potentially basal heteropterans lineages Enicocephalomorpha and Dipsocoromorpha (Insecta: Hemiptera: Heteroptera). Arthropod Systematics & Phylogeny 71(2): 103–136.

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12. Eigenständigkeitserklärung

Hiermit erkläre ich, Rico Spangenberg, geboren am 09.06.1987 in Karl-Marx-Stadt, dass ich die hier vorliegende Dissertation „The evolution of head structures in Acercaria (Insecta)“ selbstständig und nur mit den darin angegebenen Hilfsmitteln, persönlichen Mitteilungen und Quellen verfasst und an keiner anderen Fakultät oder Universität eingereicht habe. Textabschnitte von Dritten sind als solche gekennzeichnet. Ich erkläre außerdem, dass ich bisher keine Promotionsversuche unternommen habe. Darüber hinaus ist mir die Promotionsordnung der Biologisch-Pharmazeutischen Fakultät der Friedrich-Schiller-Universität Jena bekannt. Für die Anfertigung dieser Arbeit habe ich weder die Hilfe eines Promotionsberaters in Anspruch genommen, noch haben Dritte unmittelbar oder mittelbar geldwerte Leistungen von mir erhalten, die im Zusammenhang mit der hier vorliegenden Dissertation stehen. An der Erstellung der in der vorliegenden Arbeit verwendeten Originalarbeiten haben Co-Autoren mitgewirkt. Mein Eigenanteil ist für jede Arbeit einzeln angegeben.

…….. ……

Rico Spangenberg Ort, Datum